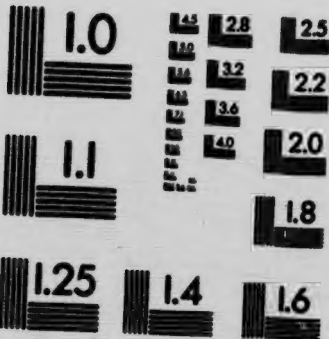


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MEMOIR 120

No. 102, GEOLOGICAL SERIES

# The Hadrosaur Edmontosaurus from the Upper Cretaceous of Alberta

BY  
Lawrence M. Lambe



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OTTAWA  
THOMAS MULVEY  
PRINTER TO THE KING'S MOST EXCELLENT MAJESTY  
1870

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1920



No. 1824



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# The Hadrosaur *Edmontosaurus* from the Upper Cretaceous of Alberta.

## INTRODUCTION.

The Hadrosauridæ<sup>1</sup> are a group of herbivorous dinosaurs of which most of the genera are from the continent of North America. The literature relative to this family is both voluminous and involved. The earlier descriptions were based often on inadequate material which gave little information as to the relations of the forms represented and their variety which has proved to be much greater than was at first supposed. The rapidity of the evolutionary changes that took place in these reptiles during Cretaceous times, especially toward the close of the period, resulting in a wonderful diversity of form, could not, in the circumstances, be fully appreciated. At the early stage of geological and palæontological investigation the horizons supplying dinosaurian remains had been only broadly determined. Geological exploration was at that time carried on, in the west particularly, under trying and arduous conditions; transportation was difficult; and rough-and-ready methods of collecting were used by parties most inadequately equipped for field work according to present day standards. It is not surprising, therefore, in spite of the brilliancy of the pioneer few who undertook palæontological investigation, and the ardour which they brought to bear on their work and by which they were upheld, that errors were not avoided. It does not detract from the excellence of their results to now find that diversity of form was not always recognized, that, for instance, generic terms were employed to include types not only widely separated by time intervals but also by very decided differences in structure.

Recent discoveries during the last six years in the Belly River and Edmonton formations on Red Deer river, Alberta, of nearly complete skeletons of several distinct types of hadrosaurs have provided excellent material for study and description, thrown much light on the osteology of the group, and opened the way for a classification of its members.

In the following pages a description of the large hadrosaur *Edmontosaurus regalis*, Lambe<sup>2</sup> from the Edmonton formation of Red Deer river, Alberta, is followed by a proposed division of the Hadrosauridæ into three subfamilies the classification being based principally on type and other material resulting from the exploratory work of vertebrate palæontological field parties of the Geological Survey, Canada, in Alberta, largely supplemented by the discoveries of the American Museum of Natural History, New York, in the same region and to the south of the International Boundary.

Of the two skeletons on which the genus *Edmontosaurus* was established in 1917, one is unique in that the majority of the bones of the head and of the remainder of the skeleton were found together naturally dis-

<sup>1</sup>The name Hadrosauridæ proposed by Cope in 1869 (1871) has precedence over Trachodontidæ used by Lydekker in 1888 and later by Marsh in 1890.

<sup>2</sup>A new genus and species of crested hadrosaur from the Edmonton formation of Alberta. *Ottawa Naturalist*, vol. XXI, No. 7, Oct. 1917, pp. 65-73, pls. II and III.



articulated, well preserved with remarkably little distortion, in a soft clayey sandstone easily removed and leaving the surface of the bones clean. This particular state of preservation provided an opportunity for study and description seldom accorded. A preservation of this nature was especially welcome in the skull as in the generality of cases the elements of the skull in dinosaurs are found in place and are not easily freed from each other. Any particular bone is largely hidden by the surrounding ones, and it is a matter of difficulty, often of impossibility, to remove it in order to see it in all its aspects. Also, when a skull is preserved with the elements in place any distortion that may have occurred is likely to affect all of the elements to a greater or less extent. In a naturally disarticulated skull, distortion when present in any particular bone is confined to the limits of that bone. With few exceptions all the drawings reproduced in this memoir in illustration of the text were made by Mr. Arthur Miles under the supervision of the writer.

#### MATERIAL ON WHICH EDMONTOSAURUS IS BASED.

*Edmontosaurus* is represented in the collections of the Geological Survey by remains, including the skull, of at least two individuals, as follows:

Collection of 1912, Edmonton formation, Red Deer river, Alberta, field No. 27, Cat. No. 2288, genotype, from opposite the mouth of Three Hills creek, at 200 feet above the level of the river: the skull figured and described in this paper, with most of the vertebrae in place back to the sixth caudal, one hind limb lacking a few phalanges, one humerus, both pubic bones together, one ischium, the greater part of the right ilium, and some ribs. Estimated length of individual considerably over 30 feet. From field measurements the length of the following bones are: femur 47 inches, humerus 27 inches, ischium 54 inches. The discovery of this specimen was made by L. Sternberg, assistant on the Geological Survey party of 1912.

Collection of 1916, Edmonton formation, Red Deer river, field No. 6, Cat. No. 2289, paratype, found by G. F. Sternberg 7 miles west and north of Morrin, in sec. 16, tp. 31, range 21, on the west side of the river, 90 feet above water level: a skeleton lacking some of the bones of the feet, the tail vertebrae behind the fifth caudal, the premaxillaries and the predentary. There is a possibility of the right ilium not being present. The bones of this individual are splendidly preserved and lay closely scattered within a grey, clayey sandstone which is easily removed leaving the surfaces in good condition. The elements composing the top of the skull are preserved together. The remaining bones of the head, including the mandibles, were found disarticulated. Femur 49 inches long, humerus 27½ inches, left ulna 30 inches, left radius 26 inches, largest right rib 50 inches along the curve, dentary 30 inches, depth of dentary in advance of base of coronoid process, from the lower surface to external alveolar border 6¼ inches.

Of the type skeleton the skull only (Figures 3 and 4) has as yet been prepared. This work was skilfully performed by L. and C. M. Sternberg.

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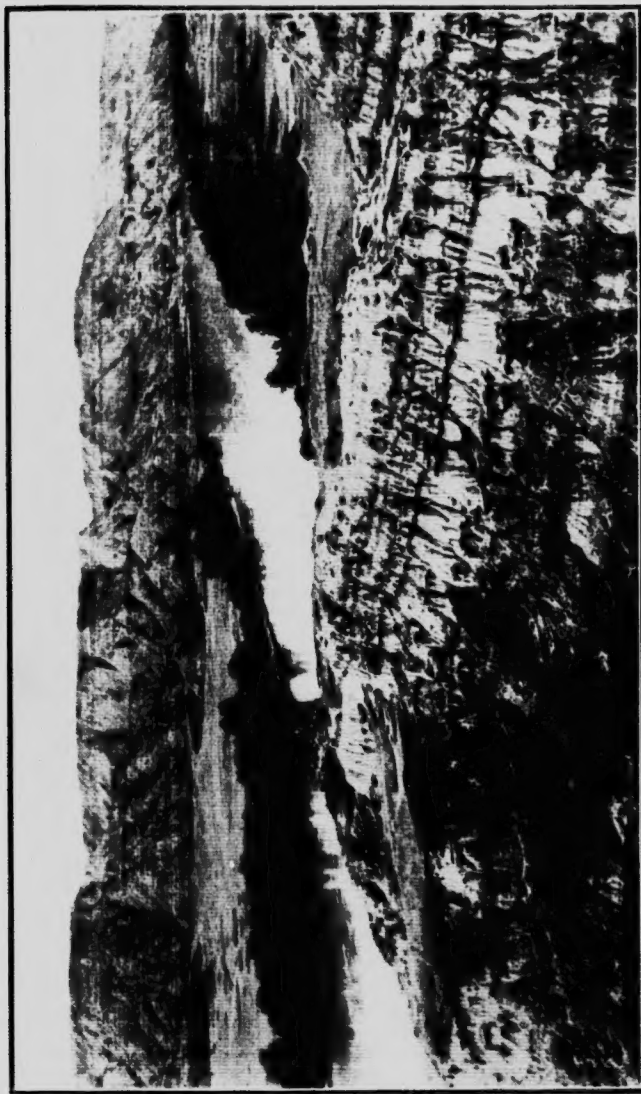


Figure 1. A typical view on Red Deer River, Alberta, showing the sandstones and clays of the Edmonton formation a few miles above where the 1916 specimen of *Edmontosaurus* was found. The beds of this formation flank the river on either side for a distance of about 100 miles. At this point the valley is 400 feet deep.



Figure 2. Site of the discovery of the 1916 specimen of *Edmontosaurus regalis* in rocks of the Edmonton formation in the valley of Red Deer river, Alberta, 7 miles west of Morrin. The banded character of the Edmonton beds is brought out well by the photograph.

The elements of the skull of the paratype, and the few vertebræ and bones of the fore limb mentioned in this report, were prepared by G. F. Sternberg who had charge of the 1916 expedition. It is hoped soon to assemble the elements of this skull and to so mount them that as many as possible will be removable for study purposes.

As the greater part of the skeleton is present in the above specimens an open mount of both is contemplated.

## OSTEOLOGY OF EDMONTOSAURUS.

### SKULL.

The skull of *Edmontosaurus* is large, massive, and long, high behind and low in front. Posteriorly it is higher than broad, anteriorly it is greatly expanded horizontally outward into a beak-like termination.

Viewed from the side its outline is subtriangular, high behind, approximately straight horizontally below, flat above behind the orbits, with a long facial slope descending rapidly forward.

As seen from above the skull is broadest in its posterior half-length, much expanded in front, and greatly constricted behind this expansion. The outline of the occiput is squarely transverse, and the margin of the snout has a semicircular curve. Behind the concavity of the anterior constriction the lateral outline is broadly convex backward.

The posterior height of the skull is greater than half its length. The maximum breadth behind exceeds the full lateral expansion of the beak, but is considerably less than the half-length. The orbit is large, as is also the narial opening. The supratemporal fossæ are of fair size, but the lateral temporal ones though high are greatly reduced in width. Concomitant with the posterior height of the skull is a long quadrate. The great development of the flattened snout is remarkable, and the depth and robustness of the mandible are equally striking.

### *Elements of the Skull Known in Edmontosaurus.*

Alisphenoid	<i>Als.</i>	Parasphenoid	<i>Pasp.</i>
Angular	<i>An.</i>	Parietal	<i>P.</i>
Articular (in part)	<i>Ar.</i>	Postfrontal	<i>Pof.</i>
Basi-occipital	<i>i. c.</i>	Predentary	<i>Pd.</i>
Basisphenoid	<i>Bs.</i>	Prefrontal	<i>Prf.</i>
Dentary	<i>Dn.</i>	Premaxillary	<i>Pmx.</i>
Ectopterygoid (Transpalatine)	<i>Ept.</i>	Presphenoid	<i>Pep.</i>
Exoccipital	<i>Ezo.</i>	Proötic	<i>Prot.</i>
Frontal	<i>F.</i>	Pterygoid	<i>Pt.</i>
Jugal	<i>J.</i>	Quadrate	<i>Q.</i>
Lachrymal	<i>L.</i>	Quadrato-jugal	<i>Qj.</i>
Maxillary	<i>Mx.</i>	Splénial	<i>Sp.</i>
Nasal	<i>N.</i>	Squamosal	<i>Sq.</i>
Opisthotic	<i>Opot.</i>	Supra-occipital	<i>Soc.</i>
Orbitosphenoid	<i>Orsp.</i>	Surangular	<i>Sa.</i>
Palatine	<i>Pal.</i>	Vomer (in part)	<i>V.</i>



Figure 3. Skull of type of Edmontosaurus, Cat. No. 2988; left lateral aspect;  $\frac{1}{2}$  natural size. *Als.*, alisphenoid; *Ar.*, articular; *Dn.*, dentary; *F.*, frontal; *J.*, jugal; *L.*, lacrimal; *lsf.*, lateral temporal fenestra; *Mx.*, maxillary; *N.*, nasal; *no.*, nasal opening; *Opot.*, opisthotic (paroccipital process); *Orb.*, orbit; *P.*, parietal; *Pd.*, palatine; *Pmx.*, premaxillary; *Prf.*, prefrontal; *Pro.*, prootic; *Pt.*, pterygoid; *Q.*, quadrate; *Qj.*, quadrato-jugal; *Sa.*, surangular; *Soc.*, supraoccipital; *Sp.*, splenial; *Sq.*, squamosal; *sf.*, supratemporal fenestra; *V.*, vomer. II, III  $\setminus$  V, exits of cranial nerves.

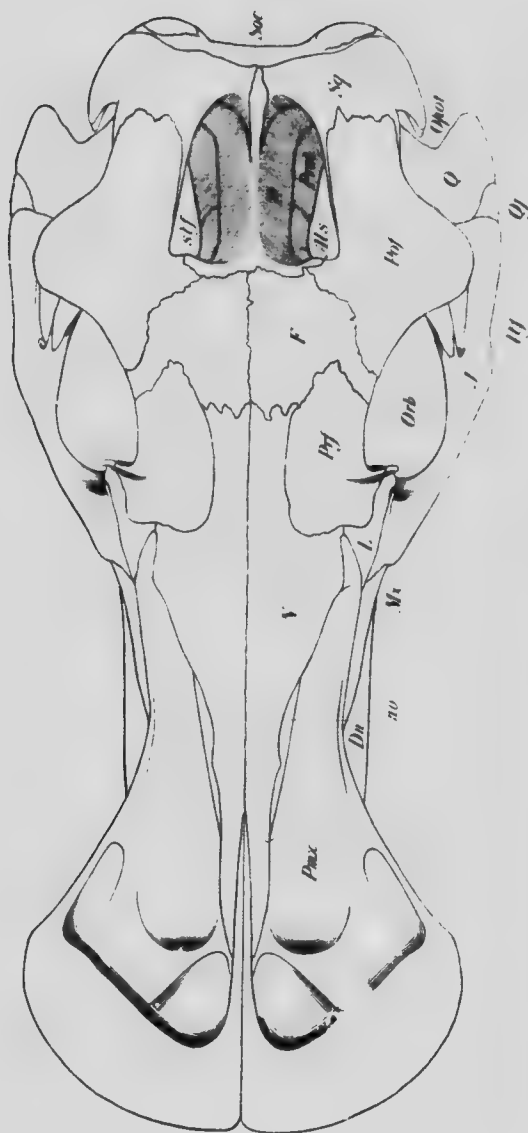


Figure 4. Skull of *Edmontosaurus*; superior aspect;  $\frac{1}{2}$  natural size. For lettering see Figure 3. This view is taken from above with the skull in the position in which it is shown in Figure 3, viz., with the line of the teeth practically horizontal.

*Cranium.* The cranium proper or brain-case of *Edmontosaurus* though small in proportion to the size of the head was strongly put together. The bones entering into its formation were thick and between many of them coössification took place; at least in the paratype, on which the present description is principally based, the brain-case, although excellently preserved with wonderful detail of structure and form, exhibits few of the sutures externally in the side walls and basicranial axis. In the brain-cavity none of the sutures have been detected.

In *Edmontosaurus*, and apparently in the Hadrosauridæ generally, ossification took place throughout the cranium, in fact the brain-case in the Hadrosauridæ appears to have been as complete as in the Ceratopsidæ, and in both groups an early closing of the sutures marked a departure from conditions in the typical reptilian skull in which the cranial elements tend to remain distinct throughout life.

In the paratype of *Edmontosaurus*, in the external surface of the sidewalls of the cranium, the suture between the alisphenoid and the proötic is preserved above the foramen ovale. In a large surface extending forward from the alisphenoid, representing the orbitosphenoid and the presphenoid no sutures are seen marking the separation of these bones from each other, although their upper boundaries are very distinctly and clearly defined, and in the case of the orbitosphenoid and the presphenoid their lower limits also.

Inferiorly the suture between the basi-occipital and the basisphenoid is visible on either side, but not near the midline, and it can be traced upward on the side walls for a short distance before trace of it is lost. Also in the occipital condyle the division between the basi-occipital and the exoccipital is clear and distinct not only beneath but externally and posteriorly as well.

An early and perfect union of the opisthotic with the exoccipital, and of the epiotic with the supraoccipital would be expected, but in the side walls behind the foramen ovale no sutures can be detected suggesting a division between any of the periotic bones. Nor is there a suggestion of the extent of the supraoccipital bone.

The cranial foramina are well preserved and, relying on them, with the aid of the few sutures that are visible, the proportionate size and relation to each other of the elements entering into the formation of the brain-case are fairly well established.

*Measurements of Skull of Type of Edmontosaurus.*

	Mm.
Length of skull measured in a straight line from the posterior edge of the exoccipital process (paroccipital) to the centre of the anterior premaxillary margin.....	1114
Horizontal length from anterior premaxillary margin to a point vertically below the preoccipital edge.....	1066
Height from level of posterior end of nasal at the midline of skull to lower surface of dentary.....	541
Height of orbit measured vertically down from centre of frontal contribution to orbital rim.....	205
Width of orbit at midheight.....	180
Length of supratemporal fossa.....	153
Maximum width of same near its anterior end.....	85
Width of infratemporal fossa toward its lower end.....	60
Length of quadrate.....	420
Breadth (antero-posterior) of external face of same at midheight.....	76





Figure 5. Cranium of Edmontosaurus, Cat. No. 2289;  $\frac{1}{2}$  natural size; inferior aspect. *Als*, alisphenoid; *Bs*, basisphenoid; *Boc*, basi-occipital; *bsp*, process of basisphenoid; *Ezo*, exoccipital; *F*, frontal; *j*, surface for jugal; *L*, lachrymal; *l. car. in.*, lower entrance of internal carotid artery; *mx*, surface for maxillary; *N*, nasal; *occ*, occipital condyle; *Opot*, opisthotic (paroccipital process); *Orsp*, orbitosphenoid; *P*, parietal; *Pasp*, parasphenoid; *pmx*, surface for upper limit of premaxillary; *Pof*, postfrontal; *Prf*, prefrontal; *Prot*, prootic; *Psp*, presphenoid; *pt*, surface for pterygoid; *q*, surface for quadrate; *Sq*, squamosal; *sqc*, squamosal cotylus; *Soc*, supra-occipital; *stf*, supra-temporal fenestra.

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Distance in a straight line from the centre (midline of skull) of the premaxillary border anteriorly to the posterior end of the upper premaxillary limb .....	380
Distance of the posterior end of the lower premaxillary limb from the same point anteriorly .....	635
Maximum breadth across the premaxillaries in front (estimated) .....	400
Height of upper end of coronoid process above lower surface of dentary .....	288

*Basi-occipital (Boc.) Figures 5, 6, and 26.* This is a robust, compact bone as broad as long but with a comparatively slight depth. As the posterior member of the basiscranial axis it is in contact supero-posteriorly with the exoccipitals, and anteriorly with the basisphenoid. Supero-anteriorly its boundaries are not seen but it comes in contact here with the proötic and no doubt also to some extent with the opisthotic. It enters largely into the formation of the occipital condyle, bounds the foramen magnum below, and, in advance of this opening its upper surface forms a large portion of the floor of the brain-cavity beneath the medulla oblongata. It supplies about five-sevenths of the articular surface of the occipital condyle, the exoccipitals between them providing the remaining two-sevenths. Its contribution to the condyle includes more than one-half of its lower surface. Viewing the bone from below, it is narrowest in advance of the condyle, broadening again to its contact with the basisphenoid where its breadth equals that of the condylar part. In front of the broad convexity of the condyle the lower surface of the bone is transversely concave, and on either side anteriorly a rugose but not particularly prominent tubercle is developed whose roughness and tumidity is continued on to the basisphenoid. The contact of the basi-occipital and the basisphenoid is seen in the paratype toward either side of the lower surface, and can be traced upward externally for a short distance. Posteriorly the basi-occipital extends back for some distance beyond a point vertically below the roof of the foramen magnum.

*Measurements of Basi-occipital of Edmontosaurus, Specimen Cat. No. 2489.*

	Mm.
Breadth inferiorly in posterior half (across condyle) .....	98
Breadth inferiorly at junction with basisphenoid, about .....	102
Length, inferiorly, about .....	100
Thickness (depth) at centre of basisphenoid contribution to occipital condyle, about .....	30
Thickness (depth) at midline in front, about .....	36

*Exoccipital (Exo.) and Opisthotic (Opo.). Figures 5, 6, 7, and 26.* The exoccipitals, the lateral elements of the occipital segment of the cranium, form the side walls of the brain-cavity in its most posterior part, bound the foramen magnum on either side, and contribute largely to the occipital condyle. They are closely united, without trace of suture, to the opisthotics with which bones they evidently effected an early and thorough fusion. In their completion of the occipital condyle externally they project freely backward and are convex inferiorly and externally; they are angulated behind, and shallowly concave internally where they form upward and backward extensions of the floor of the foramen magnum.

In the occiput the exoccipitals are thought to have been separated partly, if not wholly, by the supraoccipital, but in the absence of sutures defining the limits of the latter bone nothing definite can be said in this



Figure 6. Posterior view of cranium of Edmontosaurus. Cat. No. 2886; natural size. Boc, basioccipital; Bsf, flange of basipheneoid; Bsp, process of basipheneoid; Eoc, exoccipital; Fm, foramen magnum; Uoc, opisthotic; P, parietal; Pof, postfrontal; Pso, process of squamosal; Soc, supraoccipital; Sfl, squamosal; Sfl, supratemporal foramen; XII, foramen for twelfth nerve; acf, anterior condylar foramen.

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connexion. In *Camptosaurus* the supra-occipital bounded the foramen magnum above and in *Edmontosaurus* it is probable that it occupied the same position.

The opisthotic portion of the exoccipital-opisthotic complex extends backward, with a slight inclination upward from the horizontal, and develops posteriorly a large forwardly hooked paroccipital process directed outward and downward beneath the squamosal process which it supports and resembles somewhat in general shape, and beyond which its pointed end projects.

Above the lateral convexity of the occipital condyle is a concave surface in which are four foramina (Figures 26 and 27, IX, X, XI, jug. v, a. c. f., XII) to be referred to later, piercing the exoccipital. A strong, backwardly directed ridge, springing from the basi-occipital, bounds the convexity above and merges farther back into the lower marginal curve of the paroccipital process. Above the ridge the external surface is widely channelled longitudinally behind the fenestra ovalis (Figure 26, fen. ov.), and it is in this upper depression that the division between the opisthotic and the epiotic would be expected. In this channel was probably lodged the stapes whose anterior end closed the fenestra ovalis.

*Supra-occipital (Soc.). Figures 4, 5, and 6.* Extending back from the transversely angulated upper rim of the foramen magnum is an extensive flat surface of bone which lies between the paroccipital processes of the exoccipital and broadens backward with an inclination upward from the horizontal. No indications of sutures are found in this region and evidently the supra-occipital which would be expected here in the midline, and the exoccipitals have completely coössified. It is impossible, therefore, to determine definitely the limits of the supra-occipital, but it is thought probable that the greater part if not all of this surface is supplied by the supra-occipital and that this bone entered into the formation of the foramen magnum above, confining the exoccipitals to the flanks of the opening somewhat as in *Diclonius mirabilis* as figured by Cope (1883, pl. VII).

A definite ridge extends backward from the foramen magnum along the midline of this supposed supra-occipital surface, and anteriorly on either side of the ridge the bone is widely excavated upward behind the foramen magnum, the exoccipitals flanking the excavations externally.

The back border of this surface is straight transversely for some distance outward from the midline and then suddenly acquires a greater backward protrusion which curves evenly outward into the paroccipital process. On the upper face of the protruded border on each side are curved impressed lines (Figure 8, c) which may indicate the postero-external limit of the supra-occipital.

The anterior contact of the supra-occipital with the parietal is not seen, but posteriorly there is a space between these two bones, a low space which extends outward for a short distance, about 20 mm., from the midline beneath the squamosals.

Viewing the skull from below, its extension backward from the foramen magnum is conspicuous. A noteworthy feature, in a posterior aspect, is the lowness of the parieto-squamosal arch in comparison with its breadth, as well as the smallness of the parietal contribution to the arch. Beneath this arch, following its curve, and closely applied to it, except near the

midline, is the supra-occipito-paroccipital arch. Between the parietal and inner part of the squamosals and the hinder border of the supra-occipital, the space, representing apparently a confluence of the posttemporal fenestrae occasioned by the very limited entry of the parietal into the occiput, extends forward for at least 50 mm., beyond which it has not been possible to follow it. Issuing from either side of the space is a well-defined groove (Figure 6, *d*) in the squamosal which ascends outward to the upper surface of the bone and there disappears. Between the squamosal and the supra-occipital, and below the groove is what appears to be a foramina opening (Figure 6, *e*).

**Basisphenoid (Ba.).** Figures 5, 6, 7, and 26. This element, preceding the basi-occipital in the basiscranial axis, and constituting the inferior member of the parietal segment of the cranium, is a robust bone of distinctive shape. It is in contact behind with the basi-occipital, above with the alisphenoids and orbitosphenoids, and presumably supero-posteriorly with the prootics also, but except in front where it runs beneath the orbitosphenoids its upper boundaries cannot be made out in the material available. Anteriorly it extends forward, without trace of suture, as the parasphenoid.

In inferior aspect this bone is broad posteriorly, contracts forward, and then throws off to either side, from slightly in advance of what is considered to be its midlength, a stout process which is directed outward and slightly downward to connect with the upper border of the pterygoid between that bone's alar extensions. In front of the processes the bone narrows rapidly to the breadth of the slender parasphenoid. The outline of the bone, as seen from below, may be said to be irregularly star-shaped with five rays composed of the anterior constriction, the lateral pterygoid processes, and the postero-lateral angles, the rays represented by the processes being longer than the others.

The lower surface of the basisphenoid is crossed at about its midlength by a strong transverse ridge connecting the two processes infero-posteriorly. Behind this ridge the lower surface of the bone lies in the general plane of the basi-occipital, is transversely concave, and postero-laterally is rugosely tumid next to and supplementing the basi-occipital tubercles. The posterior slope of the transverse ridge faces backward and very slightly downward. In advance of the ridge the surface of the bone between the processes is widely concave in all directions, and is inclined strongly upward so as to face obliquely forward and downward, much as in *Iguanodon*. Medially on the ridge a small, tongue-shaped process is developed which points downward with a slight backward curve.

The pterygoid processes are flattened above and below, are thickest behind, and narrow to the front, the cross-section at the base being triangular with the apex of the triangle directed forward, and the sides lengthened. They terminate bluntly. Covering their thick, obtuse ends and extending inward with decreasing breadth for a distance of over 60 mm., on their front faces is a roughened surface denoting contact with the pterygoid. Between this articular surface and the parasphenoid the bone comes to a sharp edge.

Supero-laterally, above its contraction behind the processes for the pterygoid, it sends outward a thin, triangular, wedge-shaped flange, set at an angle to the horizontal so that its upper face is inclined forward.



FIGURE 7. Anterior view of cranium of *Edmontosaurus* (Cat. No. 2289; 1 natural size. *Als.*, alisphenoid; *Bas.*, flange of basisphenoid; *Bas.p.*, process of basisphenoid; *Ezo.*, extracipital; *F.*, frontal; *I.*, parietal; *Pusp.*, parusphenoid; *Pof.*, postfrontal; *Pof.*, process of basisphenoid; *P.*, parietal; *pt.*, surface for pterygoid; *Sq.*, squamosal; *stf.*, supraorbital foramen for internal carotid artery; *I.*, *II.*, *III.*, *IV.*, ends of cranial nerves.

This flange springs from a stout base extending from the pterygoid processes to below the foramen ovale. The outline of the base of the flange is lenticular in cross-section, with the length of the lens nearly equal to five times its breadth.

Placed well forward beneath the base of the flange is the external opening of a long, straight passage, directed upward, forward, and inward, and entering the pituitary space from below, for the transmission of the internal carotid artery. Above the flange, about midway between the anterior end of its base and the common exit for the third and fourth nerves, is a foramen for a branch of the carotid artery opening directly into the main passage. This upper opening is small and occurs within a concavity of considerable size (about 15 mm. in diameter) in the external surface of the bone. Skirting the base of the flange infero-posteriorly is a well-defined groove for the course of the artery to its entry beneath the flange.

The upper surface of the basisphenoid posteriorly forms the anterior portion of the floor of the medulla oblongata. It is here perforated by the forwardly directed passages of the sixth nerves which enter the infundibulum, one on either side of the midline, from behind. Extending down into the great thickness of the bone, in continuation of the infundibulum, is the space for the pituitary body about in line with the hinder slope of the transverse ridge connecting the pterygoid processes inferiorly.

*Measurements of Basisphenoid of Edmontosaurus, Specimen Cat. No. 2289.*

	Mm.
Infero-posterior breadth.....	110
Inferior breadth behind pterygoid processes.....	63
Breadth across pterygoid processes.....	186
Infero-anterior breadth.....	20
Thickness (depth) at midline, between origin of sixth nerves and infundibulum, to lower surface behind transverse ridge.....	66
Thickness (depth) from lower end of pituitary space to lower surface behind transverse ridge.....	37
Superior breadth below optic foramen.....	18

*Parasphenoid (Pasn.). Figures 3, 5, 7, and 26.* In *Edmontosaurus* this membrane bone is beneath the presphenoid as a forward extension from the basisphenoid with which it was evidently coalesced. It is slender, higher than broad posteriorly, and is spout-shaped in advance of the line of the olfactory nerve exit. Leading back from the spout, toward the basisphenoid, is a passage about 18 mm. high and 8 mm. wide, mostly through the parasphenoid but within the presphenoid to about one-third of its height. Whether this passage reaches the basisphenoid has not been ascertained. The suture between the parasphenoid and the presphenoid is indicated externally on both sides by a line of demarcation running forward below the level of, and nearly parallel with, the floor of the olfactory lobes.

*Alisphenoid (Als.). Figures 4, 5, 7, 8, and 26.* The alisphenoid is, in its characteristic position in the reptilian skull, in advance of the prootic, bounding the large foramen for the trigeminal nerve in front. It forms the sidewall of the brain-cavity above the hinder portion of the basisphenoid. It connects postero-superiorly with the parietal, superiorly with the frontal, and externo-superiorly with the postfrontal. Inferiorly,



fusion with the basisphenoid probably took place as the suture here not seen, also its anterior boundary is not distinguishable and its coalescence with the orbitosphenoid in front may, therefore, have been complete.

The division between the alisphenoid and the proötic is marked by a suture which descends from the floor of the supratemporal fossa and enters the foramen for the trigeminal nerve from behind in the upper curve of that opening. The parieto-alisphenoid suture runs forward, from the upper end of the proötic suture, with a slight inclination upward, and curving outward reaches the postfrontal in advance of and below the anterior border of the supratemporal fossa.

In advance of and above the foramen ovale a stout ridge is developed which running upward and outward forms an inferior angulation of the bone between the supratemporal fossa and the orbital cavity. This ridge in its upper part constitutes a buttress which reaches the postfrontal and the upper, inner margin of the opening of the spacious postfrontal pocket. The inner portion of this upper prolongation of the alisphenoid meets the frontal from below entering into the formation of the sidewall of the brain-cavity at the posterior part of the cerebrum. In advance of the lower end of the angulation of the alisphenoid the cranium is suddenly much compressed laterally and in the hinder part of the depression of the external surface thus formed which continues upward the anterior lateral compression of the basisphenoid above the pterygoid processes, is the foramen for the transmission of the third and fourth nerves about 25 mm in front of the foramen ovale.

The foramen ovale deeply notches the hinder border of the alisphenoid. The outer opening of this foramen is contracted in front, and from it a narrow groove extends forward on the external surface of the bone for the accommodation of the ophthalmic branch of the fifth nerve. This is much the same as in *Iguanodon* (Hulke, 1871, p. 203, pl. XI, and Andrews, 1897, p. 588, text fig.). The groove is present in a fragmentary cranium of "*Trachodon*" sp., from the Edmonton formation of Alberta, described and figured by Brown in 1914 (p. 547, pls. XXXVI and XXXVII). In *Triceratops* this branch of the nerve passed forward deeply embedded in the bone and found exit at some distance in advance of the common opening for the maxillary and mandibular branches.

*Orbitosphenoid* (*Orsp.*) and *Presphenoid* (*Psp.*). Figures 5, 7, and 26. As already stated the anterior limit of the alisphenoid has not been determined, but extending forward from this element is an extensive surface between the basisphenoid and the parasphenoid below, and the frontals above. The hinder part of this surface is apparently the orbitosphenoid and the forward part the presphenoid, but no sutures can be detected defining their boundaries except above and below where well-marked sutural lines are preserved.

In cranial material at present thought to be referable to *Stephanosaurus* the suture between the alisphenoid and the orbitosphenoid is clearly indicated extending from the foramina for the third and fourth nerves (in *Edmontosaurus* a single opening) upward, in advance of the buttress of the alisphenoid, to the frontal. Hay has found that in *Triceratops* the foramen for the third nerve and possibly the fourth lies in the boundary between the orbitosphenoid and the alisphenoid bones (Hay, 1909, p. 102).

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the alisphenoid lay from this particular nerve opening up in front of its angulated buttress. The area in advance of the alisphenoid, regarded as the orbitosphenoid, connects superiorly with the frontal and inferiorly with the basisphenoid. The presphenoid in front forms the floor beneath the olfactory lobes and may include that part of the area from the opening for the optic nerve to that for the first or olfactory nerves, and upward to the frontal, but the proportionate extent of the contact of the presphenoid and orbitosphenoid with the frontal is not known. Apparently the inferior connexion of the presphenoid with the basisphenoid and parasphenoid is extensive, limiting that of the orbitosphenoid with the basisphenoid. The presphenoid in its extension upward to the frontal flanks the olfactory lobes and the orifice for the exit of the olfactory nerves on either side, but whether it or the frontal encloses the opening above has not been ascertained.

*Proötic (Prot.). Figures 4, 5, 8, and 26.* This cranial element is behind the alisphenoid and in front of the epiotic and opisthotic, neither of which latter, however, are distinguishable as distinct bones in the *Edmontosaurus* skull, both, following the usual rule of cranial development in reptiles, having probably early fused, the epiotic with the supra-occipital and the opisthotic with the exoccipital. Superiorly this bone reaches the parietal, and inferiorly the basi-occipital, and possibly also the basisphenoid to a limited extent.

The proötic is pierced by the foramen for the seventh or facial nerve (VII). In front it completes the opening for the trigeminal nerve behind, and its hinder border is deeply notched by the fenestra ovalis (?+ the fenestra rotunda).

In *Edmontosaurus* (specimen, Cat. No. 2289) the suture between the proötic and the alisphenoid is shown in its upper course. It is seen to leave the foramen ovale high up in the posterior margin of the opening and to ascend, first for a short distance slightly forward, and then for a greater distance backward, to the parietal above. It is clear, therefore, from the position of the suture, that the greater part of the opening is in the alisphenoid as it is in the alligator. In the Jurassic herbivore *Camptosaurus* (Gilmore, 1909, p. 210, fig. 5) the foramen ovale is mostly in the proötic, as it is also apparently in *Triceratops*. Hay in his paper of 1909 on the skull and brain of *Triceratops* remarked that "in *Triceratops* the suture between the proötic and the alisphenoid may be provisionally drawn through the front of the foramen" (foramen ovale).

Superiorly the proötic extends outward from the parietal as part of the floor of the supratemporal fossa. At the outer edge of the floor it is angulated horizontally and overhangs the lower portion of the bone which is concave externally in a vertical direction down to the basisphenoid. This upper angulation or ridge, originating from the proötic, extends horizontally backward, parallel to a similar ridge developed in the opisthotic, and merges posteriorly in the upper face of the paroccipital process of the exoccipital. Between the two ridges the external surface is vertically concave and in this concavity the suture marking the antero-superior boundary of the opisthotic is to be looked for leading upward and backward from the fenestra ovalis. This suture is shown in this position in a cranium of "*Trachodon*" sp. figured by Osborn in 1912 (p. 18, fig. 13, Amer. Mus. No. 427).



Figure 8. Cranium of Edmontosaurus, Cat. No. 2289; 1 natural size; superior aspect. *Als*, alisphenoid; *F*, frontal; *L*, lacrimal; *N*, nasal; *Opot*, opisthotic; *P*, parietal; *Pof*, postfrontal; *Prf*, prefrontal; *Prot*, probotic; *Soc*, supra-occipital; *Sq*, squamosal.

*Parietal (P.). Figures 3, 4, 5, 6, 8, and 26.* This bone, the coalesced parietal pair, forms the roof of the brain-case from behind the cerebrum to the cerebellum, and, in the upper surface of the skull, passes backward from the frontals to the squamosals, separating the supratemporal fossæ. The parietal is longer than broad, narrow for a considerable distance in front of and behind its midlength, and expanded outwardly about equally at either end. Medially it rises between the supratemporal fossæ, with an increasing amount of lateral compression, to the plane of the upper surface of the skull as a high interfossate ridge extremely narrow above. Its lateral faces within the fossæ are concave from below upward.

Supero-anteriorly the parietal meets the frontals to the full extent of their combined posterior breadth in a zigzagged, transverse suture. Antero-externally it is in contact with the postfrontals in a short suture which, leaving the upper surface of the skull, passes down the front margin of the supratemporal fossa and runs forward for a short distance on the lower border of the same, Figure 5, *P*. Posteriorly it meets the squamosals from below in a curved transverse suture about half-way up the posterior face of the supratemporal fossa. In continuation of its median ridge it passes back narrowly, to the occiput separating the squamosals. The upper surface of this intersquamosal portion lies in the general plane of upper surface of the skull and is longitudinally channelled.

The parietal connects inferiorly with the alisphenoid in front, with the proötic farther back, and with the exoccipital behind. The sutural line marking the contact of the lower border of the parietal with the exoccipital and proötic runs forward horizontally in the floor of the supratemporal fossa. Its anterior continuation as the parieto-alisphenoid suture rises with an outward curve and terminates at the postfrontal a short distance in advance of the anterior margin of the supratemporal fossa, see Figure 5, *P—Als*.

The parietal posteriorly in its outward curve within the supratemporal fossa, at a lower level than the squamosal, enters largely into the formation of the posterior face of the opening. Inferiorly it assists the exoccipital, proötic, and alisphenoid in providing a partial floor to the opening. With a small external contribution from the postfrontal it bounds the opening in front.

A narrow, distinctly marked groove, continuous along the summit of the interfossate ridge, apparently marks the original division of the parietal pair.

*Measurements of Parietal of Specimen, Cat. No. 2289.*

	Mm.
Length along the midline above.....	198
Maximum anterior breadth within the supratemporal fossæ.....	150
Maximum posterior breadth.....	148
Height at midlength.....	57
Breadth at midlength.....	62

*Squamosal (Sq.). Figures 3, 4, 5, 6, 7, and 8.* This bone is large and with its fellow forms almost the whole of the hinder part of the upper surface of the skull. It bounds the supratemporal fossa posteriorly, enters largely into the formation of the external border of the same, and is in contact with the parietal, postfrontal, quadrate, exoccipital, and ?supra-occipital. It is broadest behind, and medially in front extensively

underlap the postfrontal. Postero-externally it sends downward and outward a large, laterally compressed process which, narrowing as it descends, curves slightly forward external to the para-occipital process of the exoccipital which supports it along its posterior curve. Posteriorly it extends inward behind the supratemporal fossa and is separated from its fellow only by the narrow, backward extension of the parietal ridge. Infero-externally toward the front it develops a short, stout process which descends with a strong forward and outward inclination on the anterior face of the quadrate. Between this process and the large posterior one the bone is excavated for the reception of the head of the quadrate.

Within the supratemporal fossa in the concavely and upwardly curved posterior face of the opening the squamosal in its inward course is above the parietal, the line of contact between the two bones being at a considerable distance below the plane of the upper surface of the skull. Internally it abuts vertically against the narrow posterior extension of the parietal and completes its enclosure of the supratemporal opening behind by a short forward prolongation on to the median bar.

The forward extension of the squamosal contributing to the formation of the supratemporal arcade is as broad as the portion of the postfrontal to the under surface of which it is applied. It is thin on its inner side and thickens outwardly to the cotylus for the quadrate. It extends forward to near the anterior border of the supratemporal fossa, and its thin inner edge together with the equally thin edge of the postfrontal forms the boundary of the opening externally.

Viewing the skull from above the posterior outline of the squamosal between the pendant process is almost transverse with only a slight curve forward. The squamosal in its upper surface curves slightly downward in its outward course from the parietal. Externally it bends rapidly downward to the descending outer face of the process. Postero-inferiorly the squamosals approach each other closely on either side of the parietal, forming an extremely narrow entry into the occiput. The posterior border of the squamosal for some distance outward from the parietal is heavy and rounded. Farther out, above the exoccipital, it becomes sharp-edged at first ending freely but in the process closely applied to and coinciding with the par-occipital process. Except along its posterior border the squamosal process is free from the para-occipital process and separated from it by a narrow space.

*Measurements of the Squamosal of Edmontosaurus, Paratype, Cat. No. 2289.*

	Mm.
Length, from posterior border to anterior termination beneath the postfrontal.....	195
Breadth, distance obliquely outward and downward from contact with parietal in posterior border to lower end of postero-external process, about.....	225
Breadth in supratemporal arcade.....	80
Thickness obliquely upward and outward at midlength of cotylus.....	50
Interio-posterior thickness (vertical) at contact with parietal.....	36
Thickness of process at about its middepth and midbreadth.....	11

*Frontal. (F.). Figures 3, 4, 5, 7, 8, 9, 11, and 26.* This element has a rather flat external surface of irregular shape, and longer than broad in about the proportion of 3 to 2. The suture along the midline between the pair is straight and well defined. Posteriorly the bone meets the

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parietal, externo-posteriorly the postfrontal, and anteriorly the nasal and prefrontal. Postero-externally it reaches the anterior margin of the supratemporal fossa at about the latter's midbreadth. Externally toward the front it extends outward between the postfrontal and prefrontal, and contributes narrowly to the formation of the orbital rim. The prefrontal and nasal together form an angular emargination of the front border, the extent of contact with the nasal being about one-third of that with the prefrontal. As viewed from below the frontal meets the prefrontal to the full extent of the latter's breadth which is equal to about three-fifths of the breadth of the frontal, the line of suture between the two running transversely inward from the orbital rim with a strongly zigzagged course. Between this contact and the longitudinal midline of the skull the frontal extends forward thinly beneath the nasal to a point nearly as far advanced as the supero-anterior edge of the prefrontal, the full fronto-nasal lapping length being about 111 mm. Beneath the nasals the frontals meet along the midline except for a short distance in front.

*Postfrontal.* (*Pof.*) *Figures 3, 4, 5, 6, 7, 8, and 26.* The postfrontal is a conspicuous bone of considerable size and is remarkable in that it develops a large fold or pocket subsidiary to the orbital cavity. Seen from above its outline is irregularly triangular with the apex of the triangle directed outward, the long base being greater than either of the other two sides. In lateral aspect its outline may also be said to be roughly triangular with the apex downward.

For one-half its length internally it is in contact with the frontal in a zigzagged suture extending from the centre of the upper curve of the orbital rim to the centre of the anterior margin of the supratemporal fossa. The posterior half of its length internally forms the outer half of the anterior margin of the supratemporal fossa and contributes largely to the formation of the outer margin of that opening. Overlapping the squamosal to near the posterior end of the supratemporal fossa it constitutes with that bone the supratemporal arcade separating the supratemporal from the infratemporal fossa.

Curving outward and downward and narrowing as it descends the postfrontal is gibbous externally to a marked degree and encloses within itself a large pocket which is a backward extension of the orbit and lies exterior to the postfrontal contribution to the postorbital bar. This pocket, opening directly forward, relegates the upper part of the postorbital bar to a position within the orbit, well removed from the exterior surface of the skull. The presence of this pocket occasions modifications of shape in the postfrontal bone, not previously described, so far as the writer is aware, in any known member of the Hadrosauridae.

The excavation of the postfrontal bone to form the postorbital pocket is extensive, measuring fully 115 mm. in fore-and-aft depth, and leaves the enveloping walls thin, particularly on the inner side, where over a considerable area the bony tissue is only about 1 mm. thick. In the external wall a thickness of from about 4 to 7 or more mm. is attained. In the sweeping inward curve infero-posteriorly the thickness averages about 5 mm. The excavation in its backward extension even enters for a short distance that part of the bone which overlaps the squamosal. Both in the roof and floor of the pocket the bone becomes thicker, especially so in the former on approaching the frontal suture; in the latter the thickening

is most marked toward the front where its downwardly curving margin is conspicuously furrowed in a fore-and-aft direction. The surface of the pocket is everywhere quite smooth.

The outer margin of the pocket is formed by the posterior curve of the orbital rim. The inner wall of the pocket thickens somewhat to form the inner margin which is straight and extends, from a point below and in advance of the antero-exterior curve of the supratemporal fossa, downward and slightly forward, continuing for a short distance below the pocket as a process representing the lower end of the postfrontal contribution to the postorbital bar. This inner margin is external and for the whole of its length to near its upper termination is in contact with the ascending process contributed by the jugal toward the formation of the postorbital bar. Postero-inferiorly the rotundity of the postfrontal encroaches on and considerably lessens the width of the infratemporal fossa in its upper half.

*Prefrontal.* (*Prf.*). Figures 3, 4, 5, 8, 9, 10, and 11. The prefrontal is about  $2\frac{1}{2}$  times as long as broad, and is broader in its anterior half than behind. From being posteriorly in the same horizontal plane with

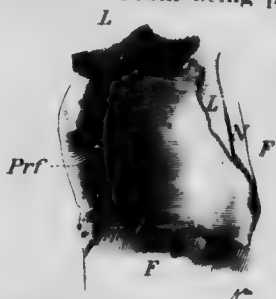


Figure 9. Right prefrontal of Edmontosaurus, Cat. No. 2289;  $\frac{1}{2}$  natural size; inferior view obliquely from behind. *F*, frontal; *L*, lachrymal; *N*, nasal; *Prf*, prefrontal.

frontal it curves convexly outward and downward anteriorly to meet the lachrymal and in so doing forms the supero-anterior portion of the orbital rim. It is bounded behind by the frontal, on its inner side extensively by the nasal, in front by the lachrymal, and below anteriorly for a short distance by the frontal bone, narrowing about equally from the sides to a point behind. The prefronto-frontal suture is sinuous and both bones are here strong and thick. In front the prefrontal overlaps the downwardly broadened portion of the nasal bone to a considerable extent, and descending also overlaps the lachrymal. The anterior end is pointed and downward and backward to the orbit the outline is broadly sinuous. In approaching the orbit from the front the bone curves rapidly outward convexly to the orbital rim. Its lower surface in front of the orbit at the latter's supero-anterior curve, is excavated, leaving the bone thin with only a slight strengthening at the orbital rim. This excavation is almost circular in outline, roughly 55 mm. in diameter, and about 22 mm. thick, forming a depression facing downward, inward, and slightly backward within the orbit in advance of the orbital rim. Externally above its midbreadth, and about half-way between its anterior end and the orbital rim is a conspicuous foramen which enters the thickness of the bone in front of the inner excavation.

The area of the inferior surface of this bone is only a little over that of its superior surface, accounted for by the extent to which it overlaps the nasal, lachrymal, and frontal above. Inferiorly the prefrontal presents a deeply concave surface, facing downward, outward, and backward between the lachrymal in front and the frontal behind. Internally it is bounded by the lachrymal for its anterior half-length, and for the remainder of the length by the nasal and frontal in nearly equal proportions, the contact of the latter, however, being the greater.



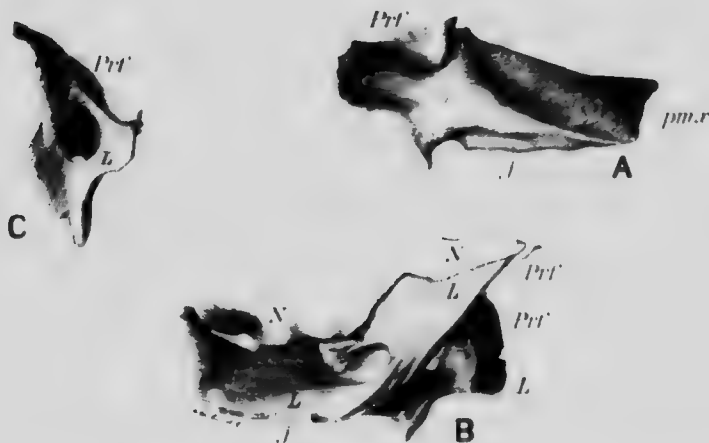


Figure 10. Right lachrymal of *Edmontosaurus*, Cat. No. 2289;  $\frac{1}{4}$  natural size. A, external aspect; B, internal aspect; C, posterior aspect; L, lachrymal; N, nasal; Prf, prefrontal; j, surface for contact with jugal; pmx, with premaxillary.

**Lachrymal (L.).** Figures 3, 4, 5, 8, 9, 10, and 11. This bone is over twice as long as high, and somewhat wedge-shaped, being thickest behind and thin toward the front. It is in contact with the nasal, prefrontal, jugal, maxillary, and premaxillary. When in position in the skull its length is in the direction of that of the lower premaxillary limb.

Viewing the lachrymal in position from without it presents a surface with an irregularly four-sided outline broadest behind and pointed in front. Supero-anteriorly it is largely hidden beneath the termination of the premaxillary limb. It is overlapped supero-posteriorly by the prefrontal for a considerable distance. Inferiorly it unites for the whole of its length with the jugal. The posterior border comes to a sharp edge which is decidedly protrudent outward in its upper part. This border is free and forms that portion of the orbital rim between the prefrontal and the jugal where it projects backward into the orbit to a considerable extent. The lachrymal contribution to the orbital rim is mostly below the midheight of the orbit. Postero-inferiorly, at the back end of the jugal contact, it extends a stout, pointed process downward behind the jugal. The external surface is somewhat convex in a direction at right angles to its length.

In the disarticulated skull, Cat. No. 2289, this bone is still firmly attached to the nasal and prefrontal, but the jugal, maxillary, and lower premaxillary limb are separate from it so that its true shape and the full extent of the majority of its surfaces are revealed. The bone ends abruptly in front with little decrease in depth forward. Outwardly the surface covered by the premaxillary limb supero-anteriorly is large, equal in area to about one-half of the entire external surface. The outer overlap of the prefrontal above is small, as is also that of the jugal below.

The inner surface of the lachrymal, revealed in the disarticulated skull, is interesting. Toward its posterior end the bone is greatly thickened

inward to a strong ridge which proceeds upward and slightly backward from the hinder end of the jugal contact, and ends thinly above between the prefrontal and the nasal at a much higher level than the posterior external limit of the bone above. In this inner thickening is a large perforation which leads forward, from the concave, interorbital posterior face of the bone, through to the free internal surface which is vertically concave, the amount of concavity decreasing forward. The thin apical portion of the maxillary fits closely from below within the lachrymal in the latter's anterior half, and continues downward the internal concavity of the lachrymal. In the description of the maxillary mention has already been made of the double foraminal opening below the internal concavity of its apex. This concavity passing from the lachrymal to the maxillary marks the course of the lachrymal canal from the large perforation in the lachrymal to the above-mentioned maxillary foramen which latter apparently connects obliquely forward and downward with the large external foramen in the maxillary situated in advance of the anterior end of the lachrymal and almost hidden by the lower border of the premaxillary limb. The internal maxillary foramen also leads backward and connects with an opening in the deep, vertical groove which is present behind the base of the apical portion of the maxillary.

In describing the type skull of *Gryposaurus*<sup>1</sup> the writer mentions the posterior opening of the lachrymal canal which has a position similar to that in the present genus.

*Measurements of Right Lachrymal of Specimen Cat. No. 2289 (disarticulated skull).*

	Mm.
Extreme external length, in a straight line.....	180
Extreme external depth.....	80
Posterior opening of lachrymal canal—	
Vertical diameter.....	40
Transverse diameter.....	23

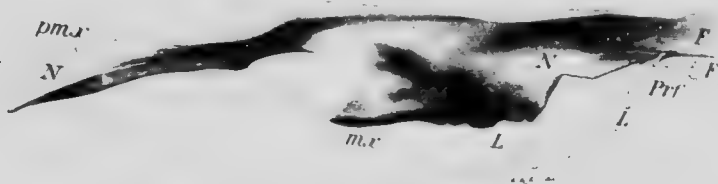


Figure 11. Right nasal of *Edmontosaurus*, Cat. No. 2289; internal aspect, obliquely from below;  $\frac{1}{2}$  natural size. F, frontal; L, lachrymal; mx, surface for maxillary; N, nasal; pmx, surface for upper limb of premaxillary; Prf, prefrontal.

*Nasal (N.). Figures 3, 4, 5, 8, 9, 10, and 11.* The nasal bone is long and narrow and is in contact with its fellow along the longitudinal midline of the skull except for about one-fourth of its length in front where the two are separated by the upper premaxillary limbs. It is slender for the whole of its length except in the anterior half of its posterior half-length where

<sup>1</sup>The Ottawa Naturalist, vol. XXVII, 1914.

it is relatively broad. Posteriorly it is in contact with the frontal which it overlaps to some extent. In its narrow posterior part it bounds the prefrontal inwardly, then suddenly expanding it extends downward in front of the prefrontal to the lachrymal and the posterior end of the lower premaxillary limb. Its contact with the lachrymal is short but it meets the premaxillary limb for a distance slightly over one-third of the latter's length. Becoming slender again it passes forward above the narial opening to meet the upper premaxillary limb and continuing forward exterior to that process it ends thinly with a rounded outline just beyond the anterior end of the opening. Along the length of its contact with the premaxillary limb the nasal thins gradually to the front in the same ratio that the premaxillary limb narrows to its posterior termination, thus providing a uniform transverse breadth to the premaxillo-nasal portion of the roof of the narial opening. Behind the termination of the upper premaxillary limb the lower border of the nasal becomes decidedly protrudent, flatly arched at its anterior end and then descending backward, as the bone rapidly expands, to the lower premaxillary limb. Retired inward from the lower end of this protrudent border a spur of bone is sent forward by the nasal within the upper edge of the premaxillary limb, and in contact with the maxillary, increasing the extent of the naso-premaxillary contact and completing the enclosure of the posterior end of the narial opening within the nasal bone as seen in lateral aspect.

*Premaxillary. (Pmx.). Figures 3 and 4.* This bone consists of an anterior portion expanding horizontally outward, a long, backwardly directed, gradually narrowing lower limb, and a relatively short upper limb also directed backward. As viewed externally it is in contact with the nasal, the lachrymal, and the maxillary. The two premaxillaries together give an anterior breadth to the snout apparently little less than the maximum breadth of the skull behind. The lower limb bounds the narial opening inferiorly for three-fourths of the latter's length, and continuing beyond the posterior end of the opening, overlapping both the nasal and the lachrymal, it terminates some distance short of the prefrontal. The upper limb passing back with increasing tenuity on the inner side of the nasal assists it in the formation of the supranarial bar to a point at about the midlength of the opening. The anterior end of the narial opening is within the premaxillary. As seen from above the front margin of the premaxillary curves outward and backward for about one-fourth of the bone's total length; the outline is then inward and backward concavely in participation of the transverse compression of the skull at and above the maxilla. The front border of the anterior expansion of the premaxillary is recurved for some distance so as to roof over an extensive cavity which opens backward. The bone throughout is thin so that what outwardly might appear to be a heavy ending to the snout is in reality greatly lightened. The floor of the cavity is smooth and is continued backward as an extensive, more or less depressed tract which is subdivided into three principal areas two of which together occupy the breadth of the bone at the mouth of the cavity and lead from it, and the third is situated beneath the narial opening. The inner anterior area is the most sunken of the three, is the least extensive, and is separated from the other two by a flange of bone which passes downward and slightly forward from the base of the upper limb in continuation of the upper

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margin of the narial opening. The outer anterior area, occupying the remainder of the bone's breadth, is bounded externally by the rounded inwardly retreating border of the expanded snout. It is not so sunken as the first but becomes moderately deep outwardly. It is marked from the subnarial area by a sharply defined difference in the amount of depression in the two. The third or subnarial area is much longer than broad, occupies the entire breadth of the lower limb, and extends at its end slightly past the narial opening. Its depressed surface, which is deep anteriorly, has an outline that, taken in conjunction with that of the narial opening, forms an irregular, lengthened oval. Its curved posterior demarcation continues downward the marginal protuberance of the nasal area referred to as occurring at the posterior end of the narial opening.

**Maxillary. (Mx.).** Figures 3, 4, 12, and 13. This element is slightly over two and a half times as long as high and in lateral aspect has roughly the outline of an isosceles triangle of which the base, represented by the straight

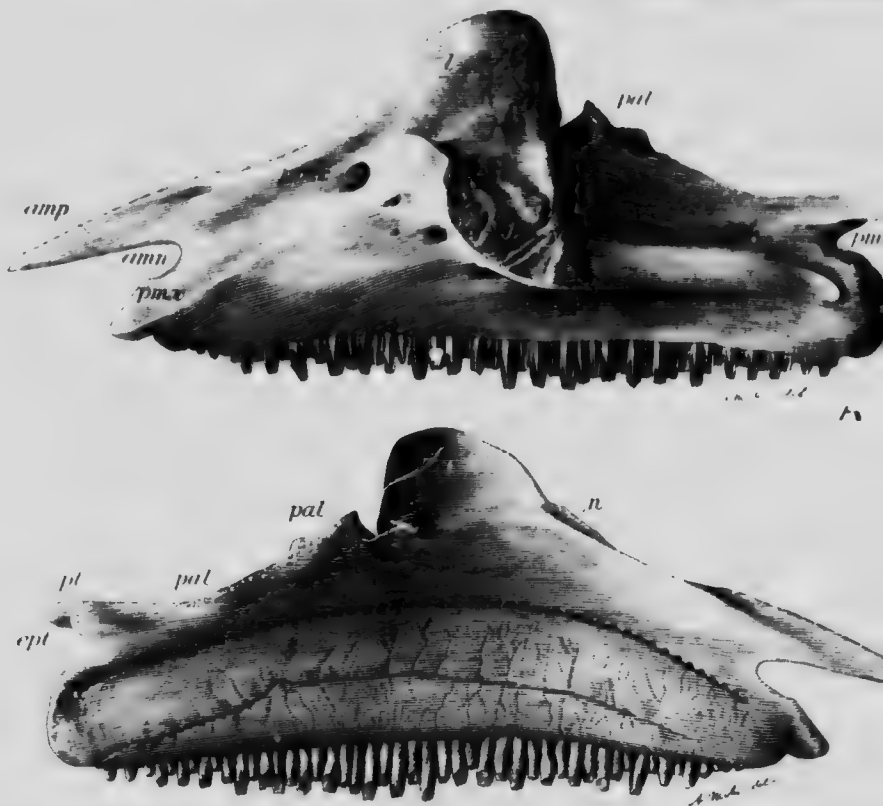
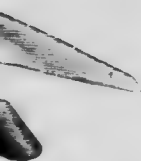
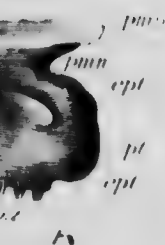


Figure 12. Left maxillary of *Edmontosaurus*, Cat. No. 2289;  $\frac{1}{2}$  natural size. A, view from without; B, view from within. amn, anterior maxillary notch; amp, anterior maxillary process; ept, surface for ectopterygoid; j, for jugal; l, for lachrymal; n, for nasal; pal, for palatine; pmn, posterior maxillary notch; pmp, posterior maxillary process; pmx, surface for lower limb of premaxillary; pt, for pterygoid.

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alveolar border, is much longer than the sloping sides, which descend concavely from a broadly curved apex. It is laterally compressed and thin above, and thick along its lower length. The inner face is as a whole rather flat in great contrast to the varied relief of the outer one. Externally the bone is most protrudent, and thickest, at about midlength at a distance above the alveolar border equal to about one-sixth of its maximum height. From here extends upward the rugose surface of attachment of the front end of the jugal, the bone thinning rapidly upward. From the lower, overhanging edge of the surface for the jugal a robust ridge runs horizontally backward with diminishing strength to near the end of the bone. The surface between the ridge and the alveolar border is vertically concave. In advance of the surface for the jugal the external face is tumid upward from the alveolar border until on approaching the antero-superior border it becomes vertically concave in a marginal depressed area in which lay the ascending lower limb of the premaxillary. This area gains in width and in the amount of its concavity as it proceeds forward causing the anterior end of the bone to be thin-edged in front and sharply angulated supero-externally. Another concave area, still more pronounced in its depression, occurs in the posterior half of the bone between the shell-like upper surface of the ridge and the postero-superior border. Unlike the anterior concave area this posterior one is widest next to the surface for the attachment of the jugal and diminishes rapidly backward leaving the hinder end of the bone thick and robust. The bone is thin in the apical region, presents a flatly convex surface outward, and is sharp-edged above. Anteriorly this apical surface descends into

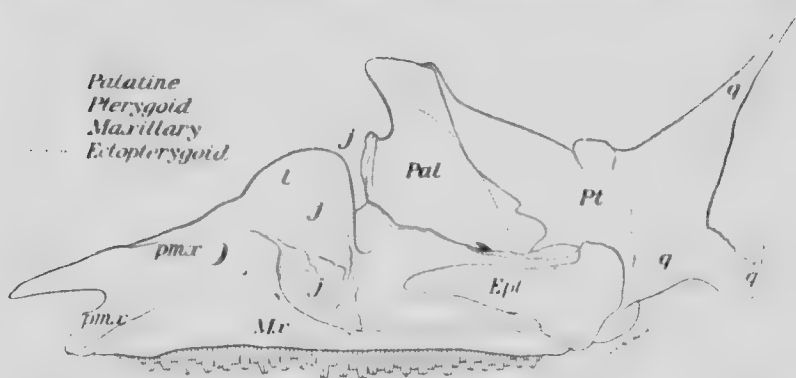


Figure 13. The left maxillary, palatine, pterygoid, and ectopterygoid of *Edmontosaurus*, Cat. No. 2289, in position relative to each other to show extent of contact;  $\frac{1}{2}$  natural size; external aspect. Ept, ectopterygoid; Mr, maxillary; l, surface for lachrymal; j, surface for jugal; Pal, palatine; pmx, surface for lower limb of premaxillary; Pt, pterygoid; q, surface for quadrate.

the antero-superior marginal depression for the reception of the premaxillary limb; posteriorly it is separated from the postero-superior concave area by a deep, vertically directed groove which emarginates the superior border behind the apex. The antero-superior portion of the apical surface is in close contact with the inner surface of the lachrymal. Below the lachrymal contact the surface for the attachment of the jugal

passes downward, becoming concave and more rugose in its lower part with a sudden increase in the thickness of the bone. The surface of the jugal is roughly semicircular in outline with the curve forward.

The antero-superior border of the maxillary is transversely narrow and is furnished with a smooth, shallow groove in which lay the inferior posterior process of the nasal directed forward below the hinder end of the nasal opening. In continuation forward of this border is a laterally compressed process (anterior maxillary process) which extends considerably beyond the main lower termination of the bone and is separated from it by a deep emargination (anterior maxillary notch). The postero-superior border of the maxilla is also narrow and supplies a very rugose surface for the attachment of the lower edge of the palatine. In continuation backward of this border occurs a posterior process between which and the heavy, rounded end of the bone is a posterior notch of small proportions than the anterior one. The postero-maxillary process receives in contact internally the pterygoid as the latter passes forward to within the palatine. It is grooved below for the upper border of the ectopterygoid in such a manner that its termination lies external to and on the ectopterygoid. The posterior notch is filled by the thick posterior portion of the ectopterygoid. The postero-external surface below the notch is rugose, curves convexly down to the level of the alveolar border and receives in close contact the ectopterygoid and below it the pterygoid the latter being overlapped by the former. The posterior end of the maxillary ridge is bounded above and behind by a groove into which fits the lower border of the ectopterygoid where it begins its rapid posterior expansion.

Although the inner face of the maxillary is flat as a whole in comparison with the outer one, the apical region is decidedly hollowed out, and there is a shallow concavity of the surface extending from the anterior end beyond past midlength. A conspicuous feature of this face is a flatly arched row of small, circular foramina openings extending below the midheight of the bone from points above the first and last teeth. There is one foramen to each vertical series of teeth. Between these dental foramina and the alveolar border is a well-defined vascular groove of the same length and with nearly the same curve as the foramina row. In the lower portion of the apical concavity are two foramina, one large, the other small, placed close together and leading downward.

There are fifty-one to fifty-three vertical series of maxillary teeth occupying seven-eighths of the total length of the bone, the dental margin terminating closer to the posterior than to the anterior end. The external and internal alveolar borders are at the same level.

Exteriorly two large foramina occur beneath the protrudent base of the surface for the attachment of the jugal, and one, even larger, is present considerably in advance of the same surface near the superior border. In the same general region are other small openings disposed as shown in Figure 12. Special reference is made to the maxillary teeth under another heading (page 55).

*Measurements of Left Maxillary of Edmontosaurus, Cat. No. 2289.*

Maximum length, about .....	M
Length at level of alveolar borders .....	

Height at midlength.....	180
Length of dental magazine.....	308
Breadth across alveolar borders at midlength.....	24
Breadth at lower edge of surface for attachment of jugal.....	70
Maximum protrusion of teeth below alveolar border at midlength of dental magazine.....	33

*Jugal. (J.). Figures 3, 4, and 14.* This element is long, thin, and plate-like, with an obtusely angulated lower outline, and deep indentations above forming the lower boundaries of the orbital and infratemporal openings. Its extreme length to its maximum depth is in about the proportion of 6 to 5. It connects antero-superiorly with the lachrymal and palatine, anteriorly with the maxillary, posteriorly with the quadrato-jugal and the quadrate, and superiorly considerably behind its midlength with the postfrontal by means of its ascending process behind the orbit. Externally it interjects a forwardly directed angulation of the front border

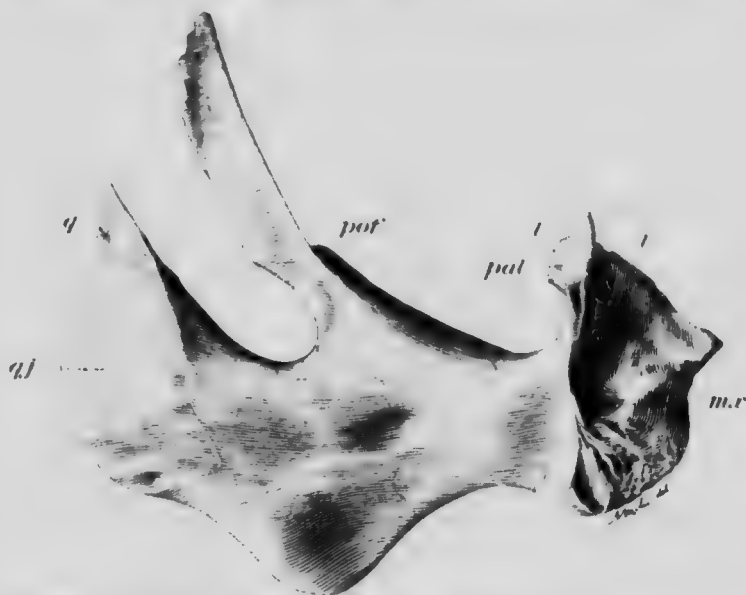


Figure 14. Left jugal of *Edmontosaurus*, Cat. No. 2289; internal aspect;  $\frac{1}{2}$  natural size. *l*, surface of contact with lachrymal; *mz*, with maxillary; *pal*, with palatine; *q*, with quadrate; *qj*, with quadrato-jugal; *pof*, with postfrontal.

between the lower end of the lachrymal and the highest point of the maxillary to the lower edge of the premaxillary limb. The anterior end of the jugal covers the maxilla behind the latter's midlength in an extensive rugose surface of contact. Antero-superiorly it is grooved in a longitudinal direction, more deeply near the orbit than toward the front, to receive the lower edge of the lachrymal. The superior border is deeply emarginated by the narrow, somewhat similarly curved, downwardly and forwardly directed lower ends of the orbit and infratemporal fossa. The ascending

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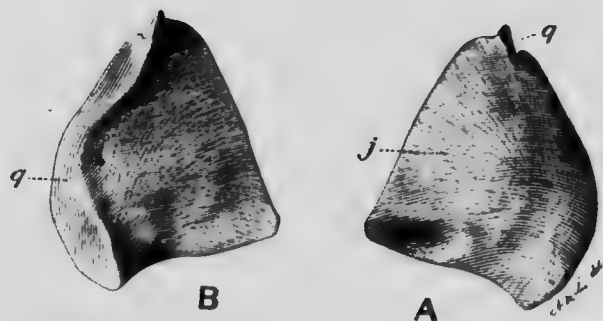


Figure 15. Left quadrato-jugal of *Edmontosaurus*, Cat. No. 2289;  $\frac{1}{2}$  natural size. *A*, outer aspect; *B*, inner aspect; *j*, surface of contact with jugal; *q*, with quadrate.

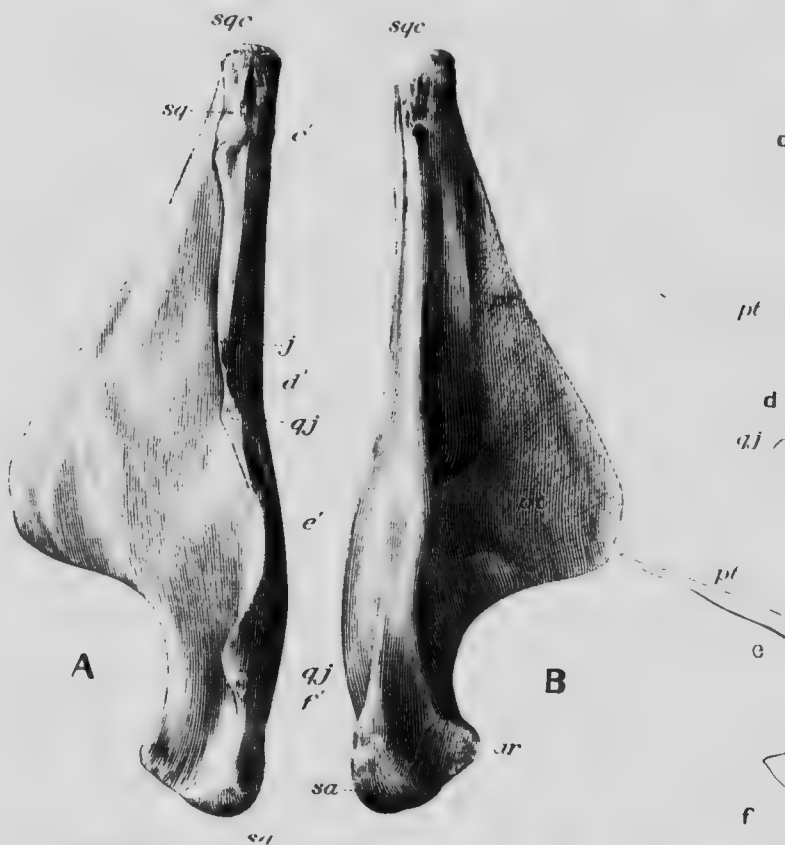


Figure 16. Left quadrate of *Edmontosaurus*, Cat. No. 2289;  $\frac{1}{2}$  natural size. *A*, external view obliquely from the front; *B*, internal view obliquely from behind; *c*, *d*, *e*, *f*, outlines of sections at *c'*, *d'*, *e'*, *f'*, respectively. *ar*, surface for articular; *j*, for jugal; *qj*, for quadrate; *pt*, for pterygoid; *sa*, for surangular (mandibular cotylus); *sq*, for squamosal; *sqc*, received in mandibular cotylus.



process, contributing to the formation of the postorbital bar, is particularly long and slender and passes up on the inner side of, and in a long contact with, the short descending process of the postfrontal and the front border of the inner wall of the postfrontal pocket. Posteriorly the jugal extensively covers the quadrato-jugal and abuts against the outer front border of the quadrate for some distance above the quadrato-jugal.

**Quadrato-jugal. (Qj.).** *Figures 3, 4, and 15.* This bone is a thin subtriangular plate, slightly higher than long, highest anteriorly and longest near the base. Its front border is straight, the lower one nearly so but undulating, and the posterior one curved forward above. It thins to the front border which is approximately vertical when the bone is in position. More than one-half of the external surface is covered by the jugal in a close, rather smooth contact lacking the numerous inequalities of the junction of the jugal with the maxillary. Posteriorly the quadrato-jugal narrowly overlaps the quadrate whose antero-external border is emarginated to receive it. A groove is developed in the border behind the apex into which the front border of the quadrate above its emargination fits.

**Quadrate. (Q.).** *Figures 3, 4, and 16.* This bone consists of a transversely compressed bar from whose inner surface a large, thin flange is directed inward and forward. It connects with the quadrato-jugal and jugal antero-externally, with the pterygoid internally by means of the flange, with the squamosal superiorly, and with the surangular and articular inferiorly. It occupies an almost vertical position in the skull with the head immovably fitted into the pit in the squamosal, and with the lower end in the mandibular cotylus.

Viewed from without it is narrowest above, and bent slightly forward from either end so as to have an evenly concave posterior outline. Below the midlength the anterior border is broadly but shallowly emarginated for the reception of the narrowly overlapping posterior curve of the quadrato-jugal. The anterior border starting from the head, with the latter's transverse thickness, becomes thin in its descent to the quadrato-jugal overlap where it thickens to some extent, but is again thin for a short distance above the lower end of the bone. In its upper part the quadrate presents a flattened surface facing outward but with a slight obliquity inward and backward, and the posterior border is obtusely angulated. Approaching midlength the external surface, with an increasing obliquity, twists inward so as to form a face directed nearly backward and ends inwardly in a narrow border which is the downward continuation of the upper posterior angulation. At the lower end the posterior surface is again angulated.

The inwardly and forwardly directed flange of the quadrate is given off from the inner surface of the main portion. Its base extends the whole length of the bone and is situated, in the lower half, about midway between the front and back borders, but toward the top it passes nearer to the back border. The flange is thin, triangular in lateral outline, and reaches its greatest protrusion in line with the centre of the quadrato-jugal contact

5329-3)

re. A, external view  
outlines of transverse  
or quadrato-jugal: pt,  
received in squamosal

or about two-thirds of its length from the upper end. Above the lower end it rises rapidly with a concavely curved edge to its apex whence it ascends less rapidly with a nearly straight edge to the head. Through it partakes of the general curve of the main portion of the bone so that its interno-posterior face is concave. Between the base of the flange and the incurved anterior border the inner surface of the bone is concave; a cavity equally deep but extending for a shorter distance above and below the midlength occurs behind the flange between its base and an incurved surface of the posterior border.

The lower end of the quadrate has its greatest diameter transverse and fits into the mandibular cotylus jointly contributed to by the surangular and the articular. When seen from below it is subtriangular in outline with the apex of the triangle inward, the base convex outward and the sides concave. The larger outer part of the lower surface is convex and faces directly downward in contact with the surangular, the inner and smaller apical portion of the surface is almost flat, looks downward and backward, and fits against the articular, the combined face being the quadrate's contribution to the mandibular hinge. The inner articular extension of the lower end acts as a pedestal for the ascending flange.

A roughened surface on the inner front of the bone, extending for a short distance downward from the head, marks the close sutural contact of the short, stout process or spur descending from the squamosal. The advance of the pit in that element into which the head of the quadrate fits.

Above the narrow, curved surface which marks the overlap of the quadrato-jugal, a limited, roughly striated area on the inner side of the anterior border indicates the surface of contact with the jugal.

The extent of the overlap by the pterygoid is well marked on the postero-internal face of the flange by a surface which extends from the top of the flange for more than two-thirds of its length. This surface extends over the flange from its edge and is roughened by striations which are approximately at right angles to the free edge. At its lower end it broadens abruptly below a conspicuous sunken area in the inner posterior marginal concavity already described.

The head of the quadrate in an undetermined species of *Trachodon* has elsewhere<sup>1</sup> been referred to as movable in the cotylus of the squamosal. There can be no doubt that it was firmly fixed in position and immovable in the genus now under description. The fact that a heavy process from the squamosal descended for some distance on and suturedly united with the anterior border of the quadrate below its head is sufficient to prove that the quadrate was stable at its upper end. The very extensive lapping contact between the quadrate and the pterygoid would in itself be sufficient to prevent any movement of the former element. The direct contact of the jugal with the quadrate was slight and can have added little to the strength of the close union of the jugal with the quadrato-jugal, and the latter with the quadrate.

<sup>1</sup>Memoirs of the American Museum of Natural History, new series, vol. I, pt. I, "Crania of *Tyrannosaurus* and *Allosaurus*," by Henry Fairfield Osborn, 1912, p. 18, fig. 13.

Measurements of Quadrate of *Edmontosaurus* (paratype, Cat. No. 2289).

	Mm.
Length of quadrate in a straight line.....	420
Maximum breadth (antero-posterior) of external surface above contact with quadrate-jugal.....	93
Horizontal distance from external surface to greatest extension inward of flange connecting with pterygoid.....	145



Figure 17. Left pterygoid of *Edmontosaurus*, Cat. No. 2289;  $\frac{1}{2}$  natural size. A, external aspect; B, internal aspect; *bsp*, surface of contact with process of basisphenoid; *ept*, with ectopterygoid; *m.r*, with maxillary; *pal*, with palatine; *q*, with quadrate.

**Pterygoid.** (Pt.). Figures 3, 13, and 17. The pterygoid is a thin bone of complicated shape in contact with the quadrate, basisphenoid, palatine, maxillary, and ectopterygoid. It probably also effects a junction supero-anteriorly with the vomer.

In lateral aspect it is roughly four-sided in outline, longest, and deep and angularly concave above, and sinuous in front and behind with convergence downward to the comparatively short base which is broad and shallowly concave.

It consists of a plate-like main portion from which is given off antero-superior alar extension and a postero-superior alar extension directed upward and forward and upward and backward respectively. Internally the bone is strengthened by two large flanges which are united above and diverge downward to opposite ends of the base.

The alar extensions, or wings, are both broad-based and narrow, rapidly upward. The posterior one is flat, continues in the plane of the main portion of the bone and ends in a slender point. The anterior one leaves the general plane of the outer face, the contained external angle approaching 130 degrees. It is curved at right angles to its length presenting a transversely convex surface facing backward and upward, and as the bone is thin, its lower, front surface is transversely concave.

Of the internal flanges the posterior one is the larger and the stoutest of the two. It is carried backward and inward in much the same general line of direction as the upper part of the anterior wing, in fact a prolongation backward of the superior border of the wing forms the joint apical portion of the converging flanges. The more anterior and thinner flange is also directed backward but more inward than the larger one, and its inner anterior surface is a continuation backward of the inner concavity of the anterior wing. The two flanges partition the bone internally into three unequal areas; an anterior one, the largest, consisting of the moderate shallow, inner concavity of the anterior wing and its backward continuation by the anterior flange; a median one, the smallest of the three, deeply confined between the upwardly converging flanges; and a posterior one, deeply but more openly enclosed by the posterior flange and the posterior wing.

The sutural union of the pterygoid with the quadrate is extensive and is effected by the application of the external face of the former to the inner face of the flange of the latter, the surface of contact on the pterygoid extending forward from the full height of its posterior border so as to include nearly the whole of the wing area and the lower portion of the bone to a short distance in advance of its inferior midlength. The slender upper end of the wing reaches up to within a short distance of the head of the quadrate, the front border of the wing and that of the flange of the quadrate being coincident for some distance down. The posterior border of the wing below its slender upper termination comes to a thin edge. Below the wing the posterior border thickens to some extent, is rugose and is applied to a ridge on the face of the flange of the quadrate. Still farther down the postero-inferior angle of the bone becomes stout, is roughened, and fits into the narrow concavity between the posterior border of the quadrate, where it is angularly most protrudent, and the base of the flange.

The pterygoid meets the maxillary in two small, separate surfaces, viz., one, infero-anteriorly where the bone curves outward and forward over the lower portion of the posterior end of the maxillary and ends pointedly, the other, a short distance higher up, where the anterior margin passes forward on the inner side of the posterior process of the maxillary.

Between this second surface for maxillary attachment and the lower part of the overlap of the flange of the quadrate is the moderately large surface for the external application of the posterior expansion of the ectopterygoid. Above the contact with the maxillary process, for the full height of the anterior wing of the pterygoid, is the surface for the palatine which passes externally back over the pterygoid for a varying distance from its anterior border.

At the midlength of the superior border, between the wings, facing inward and backward, and occupying the upper end of the posterior, internal enclosure between the posterior flange and the posterior wing is a rugose, concave surface, oval in outline, which grasps the front lower convexity of the process of the basisphenoid.

The forward end of the anterior wing of the pterygoid is not complete, but here the bone thickens slightly downward and supplies a roughened narrow surface, directed forward and facing inward, which apparently indicates the union with the back termination of the vomer.

*Measurements of Left Pterygoid of Edmontosaurus, Cat. No. 2289.*

	Mm.
Maximum length above (imperfect antero-superiorly).....	357
Maximum length below.....	184
Maximum vertical, anterior height above base-level.....	268
Maximum vertical, posterior height above base-level.....	217
Vertical height, above base-level, of superior border behind surface of contact with basisphenoid process.....	149

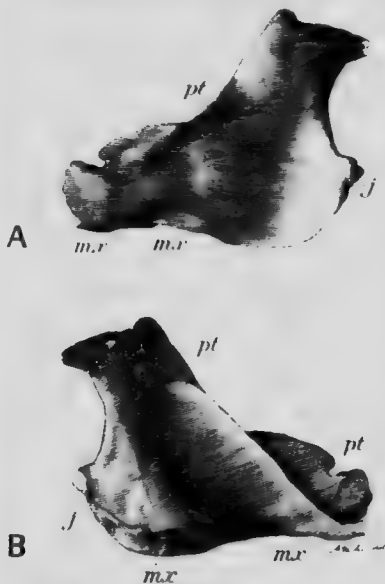


Figure 18. Right palatine of Edmontosaurus, Cat. No. 2289;  $\frac{1}{2}$  natural size. A, outer aspect; B, inner aspect; j, surface of contact with jugal; mx, with maxillary; pt, with pterygoid.

*Palatine. (Pal.). Figures 3, 13, and 18.* This element is somewhat triangular in lateral outline, is highest near the front and narrows downward and backward to the nearly straight base. It is thin and plate-like and when in position is almost vertical above the postero-superior border of the maxillary. It is suturally united to the maxillary, the jugal, and the pterygoid. The anterior border is shallowly emarginated in its upper half to form the posterior curve of the posterior nares. In the lower half of the border is a roughened sutural surface facing forward and slightly outward and downward for contact with the jugal in the infero-anterior angle of the orbital rim. This surface has an irregular or oval outline and is about twice as high as broad. Behind its contact with the jugal the palatine fits on the narrow postero-superior border of the maxillary back to and extending slightly on to the posterior maxillary process. From here

forward and upward, to the upper end of the front border, it outwardly overlaps the pterygoid, the amount of overlap being greatest toward the front and back diminishing to a simple narrow contact at the midlength of the overlap. The bone thickens near the maxillary suture and is strengthened interno-anteriorly by a smooth ridge which begins as a thickening of the anterior emargination passes down to the lower border. Behind this ridge the inner surface is broadly and shallowly concave. In advance of the ridge the bone bends outward and spreads transversely to form the jugal surface of contact. In the foremost part of its contact with the maxilla the palatine extends downward to some extent on the outer surface of the maxillary border. Infero-posteriorly the palatine develops a thin, laterally compressed, backwardly directed process between which and the main termination of the bone the border of the pterygoid ascends to its lapping contact with the palatine. Antero-superiorly the palatine apparently does not reach the vomer, the pterygoid intervening.

Maximum height of right palatine.....	Mm. 134
Maximum length of same, measured horizontally within vertical lines, about.....	185

*Ectopterygoid. (Ept.). Figures 13 and 19.* This bone is closely applied externally to the maxilla and pterygoid with its length in an antero-posterior direction. It is about twice as long as high and is thin and overlapping except in a small inwardly thickened area which fits into the postero-maxillary notch, and comes between the maxilla and pterygoid in sutural contact with both. In lateral outline it is broadest behind, narrows rapidly forward for one-third of its length, and is continued narrowly forward to its anterior end. Its external surface is gently undulating. Its anterior two-thirds of length lies closely in the postero-external concave area of the maxilla on and above the shelf formed by the horizontal ridge extending back from the maxillo-jugal surface of contact. The upper and lower borders of the bone, where it begins to broaden posteriorly, fit into two grooves in the maxillary, one in the lower surface of the postero-maxillary process, the other curving downward round the posterior end of the maxillary ridge. Here the bone thickens inwardly below the superior border and fills the maxillary notch, underlapping also the maxillary process internally to a slight extent. Below the thickened part the inner face of the bone is excavated to fit closely over the upper convexity of the posterior end of the maxillary. Posteriorly the bone broadly overlaps the pterygoid.

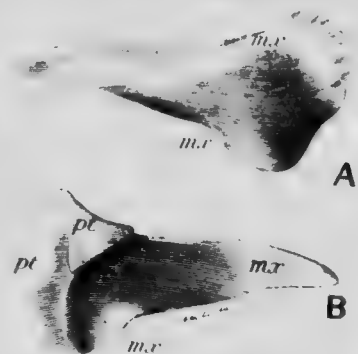


Figure 19. Left ectopterygoid of *Edmontosaurus*, Cat. No. 2289;  $\frac{1}{4}$  natural size. A, outer aspect; B, inner aspect; *mr*, surface of contact with maxillary; *pt*, with pterygoid.

## Measurements of Left Ectopterygoid of Specimen, Cat. No. 2289.

	Mm.
Estimated length.....	192
Estimated maximum breadth (height) posteriorly.....	100
Thickness of bone where it fills the postero-maxillary notch.....	23
Average thickness of bone elsewhere.....	6

**Vomer. (V.).** *Figure 3.* This element is known only from a small portion disclosed toward its anterior end in the specimen collected in 1912 (Cat. No. 2288). The vomer has not been found with the disarticulated skull, belonging to the skeleton collected in 1916. It apparently, however, connected in front with the maxillaries on the inner side of the anterior maxillary processes, and behind with the pterygoids on the interno-superior surface on the height of their anterior wings, and had an estimated length of 385 mm.

The portion of the vomer seen in the 1912 specimen is 125 mm. long, attains a maximum breadth of 20 mm., and lies in the midline of the skull in the posterior half-length of the narial opening on a level with and midway between the upper border of the lower premaxillary limbs. It is broadest at midlength, narrows slightly forward and much more so backward, so as to have an anterior breadth of 16 mm. and a posterior one of 6 mm. In front it ends abruptly in a transverse break so that the shape of the bone at the maxillary connexion is not revealed. Behind, it continues into the matrix of which as much has been removed as is at present possible. Toward the front what appears to be a median line of division, traceable for a short distance back, suggests a coalescence of an elemental pair.

The vertical inner surface of the laterally compressed anterior maxillary process in *Edmontosaurus* is rugose along the whole of its length in advance of a narrow, horizontal, shelf-like protrusion, projecting inward from the hinder part of the process, for the support of the vomer from beneath. That the vomer passed forward beyond the anterior maxillary processes is probable judging from the appearance of the inner surface of these processes which are rugosely striated to the tip. In *Prosaurolophus* a shallow groove is present on the inner side of the superior border of the lower premaxillary limb beneath the anterior end of the narial opening and just behind where the lower limbs separate for their backward ascent. This groove in *Prosaurolophus* marks the position of the attenuated anterior end of the vomer, and it is probable that the vomer of *Edmontosaurus* had a like slender termination in advance of the maxillae. To all appearances, therefore, the vomer remained narrow between the anterior processes of the maxillaries, separating them from each other by only a short transverse distance.

The shape of the posterior termination of the vomer is unknown. On the inner side of the narrowly compressed ridge forming the most elevated part of the pterygoids forward is a roughened, transversely concave surface on which the posterior end of the vomer apparently lay. Whether the vomer bifurcated behind and reached the pterygoids on either side of the median line in this manner, or united with the pair by a horizontal expansion has not been ascertained as yet. Judging, however, from the distance apart of the pterygoids anteriorly the vomer had a posterior breadth of about 50 mm. Its estimated breadth between the forward end of the anterior maxillary processes is about 10 mm. In this genus the vomer appears, therefore, to have been slender throughout and devoid of any considerable expansion.

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**Mandible.** (Figures 3 and 20.) The mandible of *Edmontosaurus* is extremely long. The converging rami meet in a short horizontal symphysis and are embraced in front by the unpaired pre-dentary bone. The rami are deepest at their midlength, and attain their maximum breadth at about two-thirds of their length from the front where the conspicuously high coronoid process is developed. In lateral aspect they have a nearly straight or slightly undulating inferior outline. As seen from above they are bow-shaped with an inward bend at midlength, and an incurve at either end abrupt in front where they meet, and less so behind where they are some distance apart. Each ramus consists of a dentary, which is edentulous for about three-eighths of its length in front, a surangular, an angular, a splenial, an articular, and possibly a prearticular, but whether this element is certainly present had not been ascertained. The dentary forms the greater part of the

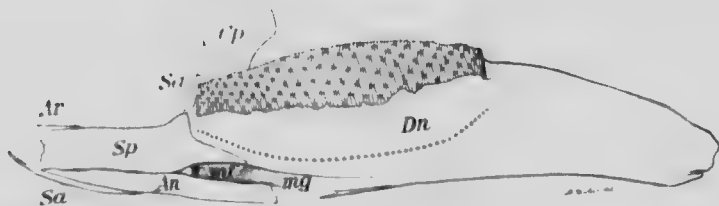


Figure 20. Left mandibular ramus of *Edmontosaurus*, Cat. No. 2289, viewed from the inner side;  $\frac{1}{2}$  natural size. An, angular; Ar, articular; Cp, coronoid process; Dn, dentary; mf, mandibular fossa; mg, Meckelian groove; Sa, surangular; Sp, splenial.

ramus. Of the other comparatively small elements, composing the hinder end of the ramus, the surangular is robust and much the largest, the angular is long and slender, and the articular the smallest. The splenial and the angular together make up the greater part of the inner surface of the ramus posteriorly. The surangular supplies the lower and outer surfaces at the hinder end. The articular lies above the surangular between it and the splenial and to a limited extent is exposed externally above the surangular. The dental magazine is nearer the posterior than the anterior end of the ramus, and is for the most part in the dentary's posterior half-length. The edentulous portion of the dentary is only slightly less than one-third of the length of the ramus.

The cotylus by means of which the mandible articulates with the quadrate is far back at a very short distance in advance of the angle of the jaw. It is provided principally by the surangular, but the articular also, to a small extent, enters infero-superiorly into its formation. The mandibular fossa is of large size and is confluent in front with the Meckelian groove which latter extends forward inferiorly on the inner surface of the dentary. The fossa is enclosed externally by the coronoid process of the dentary and the surangular, inferiorly by the dentary and the surangular, and internally by the dentary, splenial and angular. Antero-internally it opens inward through a long, narrow vacuity (internal mandibular foramen) occurring between the angular below, and the splenial and dentary above.



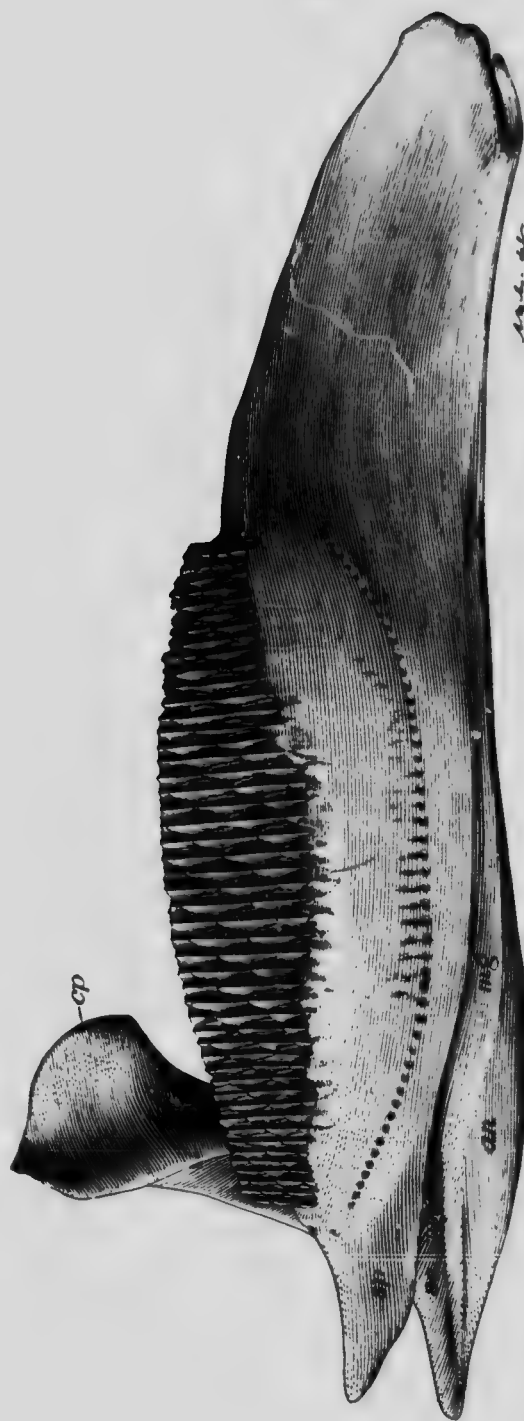


Figure 21. Left dentary of *Edmontosaurus*, Cat. No. 2289;  $\frac{1}{2}$  natural size; inner view. an, surface for angular; cp, coronoid process; ms, mandibular fossa; mo, Meckelian groove; sa, surface for surangular; sp, for splenial.

The length of the right mandibular ramus of *Edmontosaurus* (specimen Cat. No. 2289) is 910 mm.

*Dentary.* (Dn.). Figures 3, 4, 20, and 21. This element is large with three-eighths of its length in front edentulous. It is deeply excavated posteriorly by the mandibular fossa and the dental magazine occupies nearly one-half the length of the bone. The coronoid process is robust and placed far back, and gives to the dentary its maximum breadth. For the full length of the magazine the bone is deep and moderately thick. The edentulous part is comparatively thin, with a gradually lessening depth forward, and longitudinally concave internally. It curves abruptly inward in front, with a lowering of the superior border, to meet the dentary of the opposite side in a ligamentous connexion behind the prementary. The mandibular fossa excavates the coronoid process behind, and internally is continuous with the Meckelian groove which lessens in depth in its forward course near the lower border of the bone, and disappears in advance of a point in line with the front end of the magazine. Behind the magazine the dentary ends in a laterally compressed, pointed process, internal to the mandibular fossa. This process is covered on its inner face, and embraced above, by the anterior end of the splenial. Posteriorly beneath the Meckelian groove, is a narrow surface marking the internal application of the angular as far forward as a point nearly beneath the midlength of the magazine. Posteriorly below the dentary is transversely broad, thin, and obtusely pointed at its termination, underlapping the surangular so that the floor of the mandibular fossa is continuous on the upper front surface of the surangular. The narrow symphyseal surface is deeply grooved from front to back. The dental foramina, corresponding in number to the vertical series of teeth, are conspicuous internally following the lower curve of the magazine. At the anterior end externally is a rather large foramen behind which are six or seven smaller ones at irregular intervals back to the front of the magazine. Still farther back are a few other foramina in the outer face of the bone.

In the dentary there are forty-eight or forty-nine vertical series of teeth with four or five teeth and sometimes the start of a sixth in each series. The individual teeth are largest at the midlength of the magazine and decrease in size toward either end of it, the posterior ones being considerably shorter but only slightly narrower than those in front. The inner enamelled tooth-surfaces, in lateral aspect, are nearly lozenge-shaped in outline, with the longer diameter vertical, and fit closely together quincuncially in a mosaic which is almost half covered from below by the thin alveolar wall. There are about 230 teeth in each dentary, this being many less than the number (406) ascribed to *Diclonius mirabilis* by Cope in his description of that species in 1883.

*Measurements of Left Dentary of Edmontosaurus, Cat. No. 2289.*

	Mm.
Length about.....	780
Thickness at midlength and midheight of dental magazine.....	58
Distance of inner edge of cutting surface of teeth, at midlength of magazine, above lower border.....	190
Depth of bone just in advance of first vertical series of teeth.....	150
Distance of top of coronoid process above lower border of dentary.....	297
Length of dental magazine at its midheight.....	366

Posterior depth of magazine, about	60
Anterior depth of magazine, about	84
Depth of magazine at its midlength, about	115
Posterior breadth of cutting surface of teeth, about	8
Anterior breadth of cutting surface of teeth, about	8
Breadth of cutting surface of teeth at its midlength	30

**Predentary. (Pd.).** In the type of *Edmontosaurus* this bone is in place but is mostly concealed beneath the premaxillaries. Its front border is injured and throughout it seems to have been distorted and crushed. With the further removal of matrix from the specimen, if this prove feasible, some general idea of the proportions of the bone may be gained from below, but at present its description is not possible. It was broad in correspondence with the great exterior expansion of the premaxillaries, and appears to have been moderately thin in front with a development of the notches along the front border so usual in the Hadrosauridae.

In the paratype of *Edmontosaurus* the predentary as well as the premaxillaries were not found.

**Surangular. (Sa.).** Figures 3, 4, 20, and 22. In comparison with the angular, articular, and splenial, the surangular is a large, robust bone with an extensive attachment to the dentary. It, in conjunction with the angular, articular, and splenial, adds considerably to the length of the mandibular ramus, and it is principally through this bone that the attachment of the mandible to the quadrate is effected.

The surangular articulates in front with the dentary, postero-superiorly with the articular, and laterally on the inner side with the angular. It consists of a somewhat oblong main portion, longer than broad, broader in front than behind, and thick posteriorly in contrast to the anterior half-length which is thinned by having its upper surface excavated. The main portion of the bone posteriorly has a backward extension on the inner side which thins to the rear, faces upward and inward, and, when viewed from above, curves outwardly in outline to a broadly rounded termination. The supero-exterior border of this posterior extension is continued forward on the upper surface of the main portion as an upwardly directed flange which thins to the front where it ends abruptly a short distance behind the concavity in the anterior upper surface. This flange is close above, and curves in conformity with the inner border of the bone; it has a vertical inner face and a sloping outer one. Between the base of the flange and the inner border of the bone is a narrow horizontal shelf which extends forward with increasing breadth for a short distance beyond the flange and is carried back on the inner side of the extension as a groove best defined posteriorly. This shelf and groove mark the upper limit of the surface of contact between the angular and the splenial. Antero-exteriorly there is a prolongation of the main portion of the bone upward and slightly forward which ends slenderly above, reaching a height of over 110 mm., above the general plane of the lower anterior surface. This prolongation is laterally compressed throughout, and at its base is directed obliquely backward as a ridge toward the vertical flange, bounding the anterior concavity externally.

Mm.  
780  
58  
  
190  
150  
297  
366

The surangular anteriorly overlaps the thin lower posterior termination of the dentary, the excavation of the anterior portion of its upper surface forming the hinder part of the floor of the mandibular fossa. Its slender antero-exterior prolongation or limb fits closely against and runs high up on the inner side of the posterior border of the coronoid process. An impressed area of triangular outline, narrowing backward, on the lower

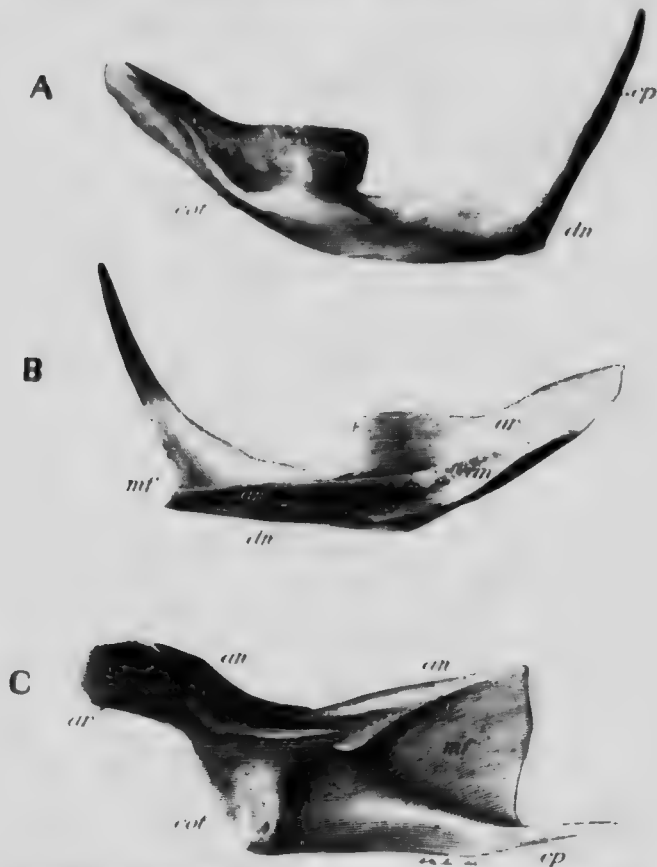


Figure 22. Right surangular of *Edmontosaurus*, Cat. No. 2259;  $\frac{1}{4}$  natural size. A, external aspect; B, internal aspect; C, superior aspect; *an*, surface for angular; *ar*, surface for articular; *col*, cotylus for distal end of quadrate; *cp*, surface for coronoid process; *dn*, for dentary; *mf*, mandibular fossa.

surface of the bone in its anterior half, and continuing upward as a decided flattening of the limb on its outer side, marks the full extent of the contact of the surangular with the dentary. The inner backward extension is closely applied from beneath to the articular which, in its more posterior part, is between this extension of the surangular and the splenial, and

which apparently passes forward on the inner side of the flange and is supported below by the narrow horizontal shelf between the base of the flange and the sutural surface for the angular.

The upper surface of the bone externo-posteriorly is shallowly excavated for the reception of the greater portion of the lower end of the quadrate, the remaining part of the cotylus being supplied by the articular. The contribution given to the cotylus by the surangular passes inward and upward on to the flange and is defined in front by a low, rounded ridge which runs transversely outward from the flange near its anterior ending to the outer border slightly in advance of the postero-exterior angle of the main portion of the bone.

*Measurements of Right Surangular of Edmontosaurus, Cat. No. 2289 (disarticulated skull).*

	Mm.
Length of bone measured along the curve of its lower surface from the front border to the termination of the posterior extension.....	290
Breadth at midlength.....	81
Height at midlength from lower surface to top of median flange.....	69
Backward extension of surangular beyond infero-posterior termination of dentary.....	147
Thickness, from lower to upper surface, of main portion of midbreadth slightly behind midlength.....	31

*Articular. (Ar.). Figures 20 and 23.* In this species the articular is as yet imperfectly known. In the type skull, Cat. No. 2288, it is represented in the right mandibular ramus by a small fragment in place between the surangular and the splenial above the posterior termination of the angular. In the disarticulated skull, Cat. No. 2289, the only part of it

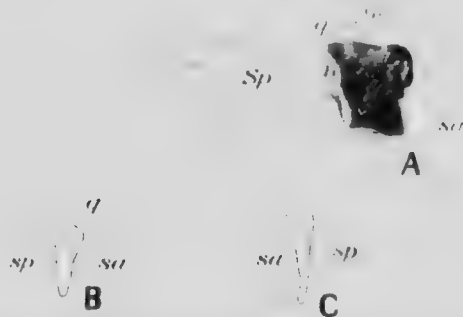


Figure 23. Portion of left articular of Edmontosaurus, Cat. No. 2289, in place on the splenial;  $\frac{1}{2}$  natural size. A, external aspect; B, anterior aspect in outline; C, posterior aspect in outline. Ar, articular; q, surface for contact with quadrate; sa, surface for surangular; Sp, splenial; sp, surface for splenial.

remaining is a piece of irregular shape, 55 mm. in maximum length, 51 mm. in depth behind, and 21 mm. in breadth antero-superiorly, adhering to and in its proper relative position to the outer posterior surface of the left splenial as shown in Figure 23. The fragment in the type skull, so far as its smallness permits, corroborates the larger portion in the second skull as regards shape and position.

The portion of the articular preserved in the disarticulated skull, although imperfect behind and possibly in front gives the depth and thickness of the bone apparently where it is stoutest. It is thinnest below and rises on its inner side slightly above the upper border of the splenial. Outwardly it displays a flattened surface directed obliquely downward, for attachment to the surangular, and having a depth equal to about two-thirds of the total depth of the bone. Above this surface is the remaining one-third of the depth of the bone directed outward, and supplying a free surface which in its anterior part is slightly concave and constitutes the small contribution of the articular to the mandibular cotylus. The narrow lower border of the articular fits into the groove in the surangular mentioned in the description of that bone as occurring above the posterior end of its surface for the attachment of the angular. Continuing backward the articular probably rose still higher above the upper border of the splenial, as restored in Figure 20, reliance being placed to some extent on the shape of the articular in *Gryposaurus*. The articular in advance of its contribution to the cotylus, in view of the fact that there is a space left between the splenial and the surangular when these bones are in position, may have continued forward as a moderately thin bone between the inner vertical face of the flange of the surangular and the concave outer surface of the splenial, and supported below by the horizontal shelf of the surangular. However, the possibility of the presence of a prearticular should not be overlooked.

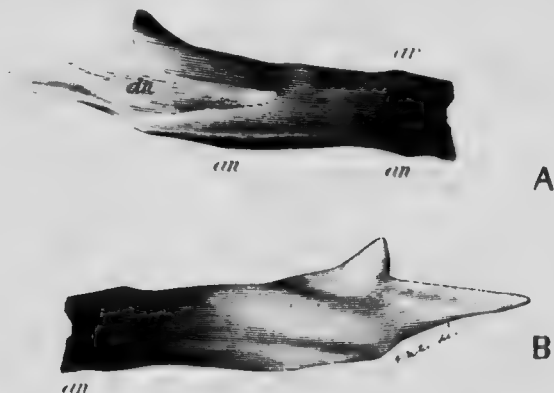


Figure 24. Left splenial of *Edmontosaurus*, Cat. No. 2289;  $\frac{1}{2}$  natural size. A, outer view; B, inner view; an, surface for angular; ar, surface for articular; dn, surface for dentary.

*Splenial.* (Sp.). Figures 20 and 24. This element is a moderately thin plate of bone of about the same general thickness as the angular but deeper and shorter, and is in contact with the angular, the dentary, and the articular, inferiorly with the angular, antero-externally with the dentary, and postero-externally with the articular.

It is deepest at about one-third of its length from the front where a thin process, developed from the superior border, curves outwardly over the supero-internal termination of the dentary behind the dental magazine.

In advance of the curved process the bone narrows to a point. In the posterior two-thirds of its length it lessens but slightly in depth backward. In each of the three splenials available for study, viz., the two belonging to the naturally disarticulated skull, Cat. No. 2289, and the right one of Cat. No. 2288, the posterior end is missing, but, judging principally from the shape of the surangular in this region, it probably terminated with a rounded lateral outline as restored in the above figure. The bone is curved in conformity with the curve of the angular and surangular so that its inner surface is moderately concave in a longitudinal direction.

Its superior border toward the front rises over, as already stated, and embraces the upper edge of the dentary. Its pointed anterior extension reaches forward and is applied to the dentary below the hindermost portion of the row of dental foramina. The surface of contact with the dentary extends slightly back of the splenial's half-length.

The splenial reaches farther back than the angular and is in contact inferiorly with it for nearly the whole of the latter's half-length. The surface of contact between the two is broadened and, with the increase in area, strengthened by a ridge which extends outward along its length causing the lower external surface of the bone to be decidedly concave in a vertical direction. The upper surface of this ridge receives, and supports from below, at least in its more posterior part, the lower border of the articular. Anteriorly there is a space left between the splenial's pointed extension and the angular which leads outwardly into the mandibular fossa. Postero-externally the bone for the whole of its depth is applied to the articular and passes beneath it by means of the ridge just mentioned.

*Measurements of Left Splenial of Edmontosaurus, Cat. No. 2289 (disarticulated skull).*

	Mm.
Length of bone preserved, measured along the inner curve.....	250
Estimated total length.....	304
Depth at midlength.....	50
Length of sutural surface of contact with dentary.....	172
Maximum breadth of same.....	16



Figure 25. Right angular of Edmontosaurus, Cat. No. 2289;  $\frac{1}{2}$  natural size. A, external aspect; B, internal aspect; da, surface for dentary; sa, for surangular; sp, for splenial.

**Angular. (An.).** *Figures 20 and 25.* This bone is long, narrow, and thin, and is in sutural contact with the splenial, the surangular, and

the dentary. It runs forward from a short distance in advance of the hinder end of the surangular, on the inner side of that bone, to a point on the dentary below the Meckelian groove, presumably about in line with the midlength of the dental magazine. In lateral aspect it is bent at one-third of its length from the posterior termination, being straight and inclined slightly upward in the hinder part, and horizontally straight in the two-thirds forward length. Its greatest depth is at the bend whence it narrows forward and backward to its pointed ends. Viewed from above it has a flattened sigmoid curve resulting from its close application posteriorly to the convex curve of the inner border of the surangular, and anteriorly to the longitudinal concavity of the lowermost inner surface of the dentary. Superiorly, for nearly the whole of its posterior half-length, it is in contact with the lower border of the splenial (fig. 25B, representing the inner aspect of the right angular, the contact of the bone with the three elements above mentioned are clearly indicated.

*Measurements of Right Angular of Edmontosaurus, Cat. No. 2289 (disarticulated skull).*

	Mm.
Length of bone preserved, measured along the inner curve.....	290
Estimated total length.....	377
Depth at bend.....	37
Maximum horizontal breadth of sutural surface for surangular (max. thickness).....	15

*Outer Openings of Skull.*

*Supratemporal Fossæ.* These openings are of moderate size, and very close together on either side of the extremely narrow longitudinal parietal ridge. They are subtriangular in outline, more than twice as long as wide, narrowly rounded behind, and end squarely in front where they are widest. They are bounded externally by the postfrontal and squamosal (supratemporal arcade), posteriorly by the squamosal, anteriorly by the postfrontal and parietal, and internally by the parietal and squamosal. They are floored on their inner side by the parietal, proötic, and to a limited extent also toward the front by the alisphenoid. Infero-externally they open beneath the supratemporal arcade into the infratemporal fossæ, and are confluent infero-anteriorly with the orbital cavities.

*Infratemporal Fossæ.* The principal feature of these openings is their extreme narrowness in comparison with their height. Although narrow below they become still further reduced in their upper half where they are encroached on by the backward extension of the large postfrontals. Their lower end is within the jugal. Anteriorly the fossæ are bounded by the post-orbital bar proper and the augmented postfrontal; their narrow upper end is confined by the postfrontal and squamosal, and posteriorly their margin is formed by the squamosal, quadrate, and jugal. They are nearly twice as long as the supratemporal fossæ.

*Orbital Cavities.* The orbits are the largest of the openings of the skull, the next in size being the narial opening. They are subcircular in outline with an antero-inferior extension downward and forward, the height slightly exceeding the length at midheight. The anterior margin is formed by the prefrontal, lachrymal, and jugal. Superiorly the opening is bounded by the prefrontal, frontal, and postfrontal, posteriorly by the



postfrontal and jugal, and inferiorly by the jugal. The relative sizes of the orbits, narial opening, infratemporal fossæ, and supratemporal fossæ, may be expressed by the numbers 86, 56, 25, and 24 respectively.

*Post-temporal Fossæ.* In the occiput a deep transverse indentation or groove runs outward on either side from beneath the backward extension of the parietals under the lower border of the squamosal. This groove for some distance beneath the squamosal (Figure 6) represents the post-temporal fossæ reduced vertically to such an extent as to be virtually closed. In its more external part the lower border of the squamosal has an arched curve above the groove. Inferiorly the groove is bounded by the prootic and supra-occipital. A somewhat similar condition of these fossæ is found in *Iguanodon*.<sup>1</sup>

*Narial Opening.* This opening has the form in lateral outline roughly of a lengthened oval, somewhat flattened below, and more rounded in front than behind, with a length nearly five times the height. The anterior and posterior ends are within the premaxillary and the nasal respectively. The superior margin is formed almost wholly by the nasal, and the inferior one principally by the premaxillary. The size of the opening is proportionate to the great anterior development of the premaxillaries.

*Foramen Magnum.* This opening is large in comparison with the size of the brain-cavity. Its width is equal to half that of the cavity at the cerebrum and about equal to that across the medulla. It is nearly oval in outline, higher than wide, and narrowed slightly below. The vertical diameter is 50 mm. and the horizontal one at midheight about 40 mm. It is bounded below by the basi-occipital, laterally by the exoccipitals, and above apparently by the supra-occipital. Its upper outline is sharply defined by the transverse angulation formed by the junction of the descending roof of the brain-cavity and the lower surface of the supra-occipital. Laterally and inferiorly its exact boundary is not so clearly marked—being carried backward over the basi-occipital and between the condylar protrusions of the exoccipitals. Viewing the cranium from behind the opening is set deeply in the occiput with the supra-occipital extending nearly horizontally backward for a distance of fully 115 mm. from its upper rim.

*Cranial Foramina.* Figures 26 and 27. The openings in the brain-case for the exit of the various nerves are well preserved in the paratype of *Edmontosaurus*. Their size and position are as depicted in Figure 26 giving an external view from the right of the cranium proper. In Figure 27 showing the cast of the brain-cavity in three aspects, lateral (A), superior (B), and inferior (C), the length of the foramina and their direction through the cranial walls are indicated.

The olfactory nerve opening (I) is bounded inferiorly and externally by the presphenoid. Whether the opening is roofed over by the frontals, or by the presphenoid, or by both, has not been determined as no sutures giving the desired information are preserved. The side walls of the presphenoid seem to curve inward over the opening, in which case the frontals would contribute to the formation of the roof only along the longitudinal midline. The opening is more than twice as wide as high.

<sup>1</sup>Quatrième note sur les dinosaures de Bernissart, par M. L. Dollo, Bull. Musée Royal d'Histoire Naturelle de Belgique, tome II, 1883, pp. 224-248, pls. IX and X.



Figure 26. Brain-case of Edmontosaurus, Cat. No. 2289;  $\frac{1}{2}$  natural size; right lateral aspect. *acf*, anterior condylar foramen; *Als*, alisphenoid; *Boc*, basi-occipital; *Bs*, basisphenoid; *Bsfl*, flange of basisphenoid; *Bsp*, process of basisphenoid; *Exo*, exoccipital; *F*, frontal; *jug. v.*, foramen for jugular vein; *l. car. in.*, lower posterior foramen for internal carotid artery; *Opot*, opisthotic; *Orsp*, orbitosphenoid; *P*, parietal; *Pasp*, paraspphenoid; *Pof*, postfrontal; *Prot.protic*, prootic process of squamosal; *sq*, squamosal; *sf*, supratemporal fossa; *u, car. in.*, upper (anterior) foramen for internal carotid artery; I, II, III, IV, V, VII, VIII, IX, X, XI, and XII, exits of cranial nerves.

Its outline, as seen from the front, is flat below with a slight, abrupt rise at midwidth, rounded at either side, and broadly lowered medially above, so that the height is least at the middle, indicating the position of the olfactory lobes, one at either side.

Piercing the cranium from side to side where it is narrowest in the lower part of the orbitosphenoids is a passage of considerable size vertically in line with the anterior end of the basisphenoid. This passage occupied by the optic chiasma also communicates widely upward with the brain-cavity through the floor below the space for the cerebrum; it is in advance of, and at a slightly higher level than the pituitary fossa with which it is confluent behind. The external openings of the passage are oblique to the longitudinal axis of the skull, and set at an angle to each other, approaching each other in front, and facing decidedly downward and forward. They are oval in outline and nearly twice as long as high. The median opening above is 30 mm. wide transversely. It was by means of the lateral openings that the optic nerves (II) found exit.

Behind and at a slightly lower level than the transverse perforation just described, and separated from it by a bar of bone about 14 mm. broad, is a large, almost circular foramen apparently for the common exit of the oculomotor (III) and trochlear (IV) nerves. It occurs in the back part of the decided concavity marking the lateral compression of the lower, front portion of the brain-case. It opens through the upper part of the side walls of the pituitary cavity (infundibulum) its upper curve being about on a level with the posterior rim of the pituitary fossa. Running forward from the lower margin of the foramen is the suture defining the upper limit of the front part of the basisphenoid. Whether this opening is wholly within the alisphenoid, or, as its position suggests, bounded behind by the alisphenoid and in front by the orbitosphenoid has not been determined, complete coalescence between these two elements having apparently taken place.

Behind the foramen for the third and fourth cranial nerves, at a somewhat higher level and separated from it by a space of about 27 mm., is an opening of large size, the foramen ovale or trigeminal nerve (V) exit. This foramen occupies its characteristic position in the reptilian skull in front of the proötic. It lies for the most part within the alisphenoid with the proötic bounding it posteriorly, and is a short distance above the hinder end of the base of the flange directed outward from the upper portion of the basisphenoid. Its outer opening is larger than the inner one but its greatest diameter is attained within the thickness of the bone where the size of its passage through is considerably increased by excavation forming a fossa.

This foramen is best preserved on the right side in the paratype of *Edmontosaurus* where externally it is longer than high, subtriangular in outline and highest in front, measuring 24 mm. in length and 18 mm. in height. On the left side of the specimen the opening has been reduced in height by crushing. Leading forward from it anteriorly is an open channel or groove which marks the position of the ophthalmic branch of the trigeminal nerve (V) (see also p. 52). The suture between the alisphenoid and the proötic reaches the opening posteriorly from above.

In the floor of the brain-cavity, midway between and at a slightly lower level than the trigeminal nerve (V) exits, are two small openings,

one on either side of the longitudinal midline of the floor, which mark the origin of the abducent or sixth nerve from the ventral region of the medulla. From each of these openings a long, straight passage leads forward with a downward inclination into the pituitary cavity debouching immediately below the hinder rim of the pituitary fossa, and in close proximity to the foramen for the third and fourth nerves. The two passages are parallel to each other and pierce the basisphenoid in its median elevation behind the pituitary fossa. From the position of the anterior end of these passages it is presumed that the sixth nerve, a purely motor nerve supplying the external rectus muscle of the eye, found exit also from the large aperture apportioned to nerves III and IV.

The foramen for the seventh or facial nerve, behind the foramen ovale, and separated externally from it by a surface of bone measuring about 11 mm. across, is small and inconspicuous. A narrow but well-defined channel leads downward and forward from it toward the deep groove, beneath the flange of the basisphenoid, which terminates below at the lower entrance of the internal carotid artery. This foramen pierces the proötic as in the alligator.

Behind the exit of the seventh nerve, and distant from it externally about 16 mm., is a rather large opening, the fenestra ovalis + the fenestra rotunda, which internally communicates directly inward with the brain cavity by a small oval aperture, the internal auditory meatus, through which the eighth or auditory nerve left the brain and reached the auditory organ by means of its various branches. Rising upward in the thickness of the bone from the passage between the outer opening and the internal meatus is a large space which apparently marks the position of the labyrinth. The semicircular canals are not preserved in the specimen (paratype) nor has it been possible to detect any representation of other parts of the auditory organ. The side wall of the brain-case is thickened inwardly at this position of the labyrinth causing a marked convexity of the surface of the bone in the brain-cavity over a considerable area above the internal auditory meatus. At about the middle of this convex area, at about 10 mm. above the meatus is a small opening, between 2 and 3 mm. wide, connecting the large space within the bone with the brain-cavity.

Four foramina of rather small but nearly equal size occupy a definite sunken area bounded below by the lateral convexity of the occipital condyle, and in front and above by a prominent ridge which latter runs upward from the basi-occipital behind the fenestra ovalis and continues almost horizontally backward to the paroccipital process of the exoccipital. This sunken area is most depressed in front where it ends as an excavation beneath the ridge. Of the four foramina two are close together in front, one above the other, and are overhung by the ridge and partly concealed by it in a lateral view of the skull. Anteriorly the ridge is sharp-edged behind and about 12 mm. broad. The third foramen is at a short distance behind the front pair, and the fourth follows the third at a somewhat increased interval. The lower anterior opening and the two posterior ones are in an almost straight line horizontally. The upper of the two front apertures, slightly larger than the lower one, is the foramen lacerum posterius transmitting the glossopharyngeal (IX), the pneumogastric (X), and the spinal accessory nerves. The direction of the passage outward through the bone for these nerves is obliquely backward. The inner end

of the passage is large and close behind the internal auditory meatus, the external one is much smaller and opens under the ridge already mentioned about 9 mm. distant from the back margin of the fenestra ovalis. The lower opening is for the transmission of the jugular vein. The passage for this vein starts within the wall of the brain-cavity in a small orifice well down in the medullary region some distance beneath the inner end of the foramen lacerum posterius. It curves upward and backward through the bone and emerges close beneath the common exit of the ninth, tenth, and eleventh nerves, separated from it only by a thin partition of bone so that the two openings are almost confluent externally. Near the external end of the jugular passage there seems to be a branch leading forward within the bone, but it is small and its course has not been ascertained. The opening behind the foramen lacerum posterius, and distant from it about 8 mm., is the anterior condyloid foramen, Figures 26 and 27, *a, c, f*. The hindmost of the foramina, about 16 mm. farther back, is the exit of the twelfth or hypoglossal nerve (XII). Its inner end is considerably larger than the outer one.

*Brain. (Figure 27.)*

The brain-cavity of *Edmontosaurus* is long and narrow but relatively much broader across the cerebrum than elsewhere. Its length is slightly less than one-fourth that of the skull, and it is both actually and proportionately longer than the brain-cavity of *Claosaurus annectens* as represented by Marsh's figure of the cast.

In the paratype of *Edmontosaurus* there is little distortion in the cranium and an accurate gelatine cast of the entire brain-cavity was obtained and reproduced in plaster, Figure 27, *A, B, C*. The cast includes the nerve exits for their full extent outward, giving the diameter, direction, and length of the passages, and the thickness of the walls of the brain-case at any particular opening.

The shape of the brain-cavity probably does not give exactly that of the brain itself especially if conditions were at all similar to those found in the Tuatara (*Sphenodon punctatus*) of New Zealand. Dendy<sup>1</sup> has remarked on the great disparity in size in *Sphenodon* between the brain-cavity and the brain, which latter he found to be suspended in the cavity by innumerable strands of connective tissue. It is reasonable to suppose, however, that in dinosaurs the brain conformed in a moderate degree to the shape of the cavity, and this assumption appears to be borne out by the cast in which the various divisions of the brain seem to be fairly represented as regards size and relief. In describing the cast of the brain-cavity of *Edmontosaurus*, therefore, its different parts will be referred to in terms that would be applied to the brain itself.

In Figure 27, the cast is shown in lateral, *A*, superior, *B*, and inferior, *C*, aspects. In it the principal divisions of the brain are denoted, viz., the olfactory lobes, the cerebrum (cerebral hemispheres), the optic lobes, the cerebellum, the medulla oblongata, and the pituitary body. All the cranial nerve exits are represented, as well as the internal carotid artery's entry into the pituitary body from below. Two constrictions are con-

<sup>1</sup>Philos. Trans. Royal Soc. London, Ser. B. vol. 201, 1911, pp. 227-331. "On the structure, development, and morphological interpretation of the pineal organs and adjacent parts of the brain in the Tuatara (*Sphenodon punctatus*)," by Arthur Dendy.

spicuous, one behind the cerebrum, the other separating the cerebellum and optic lobes from the medulla.

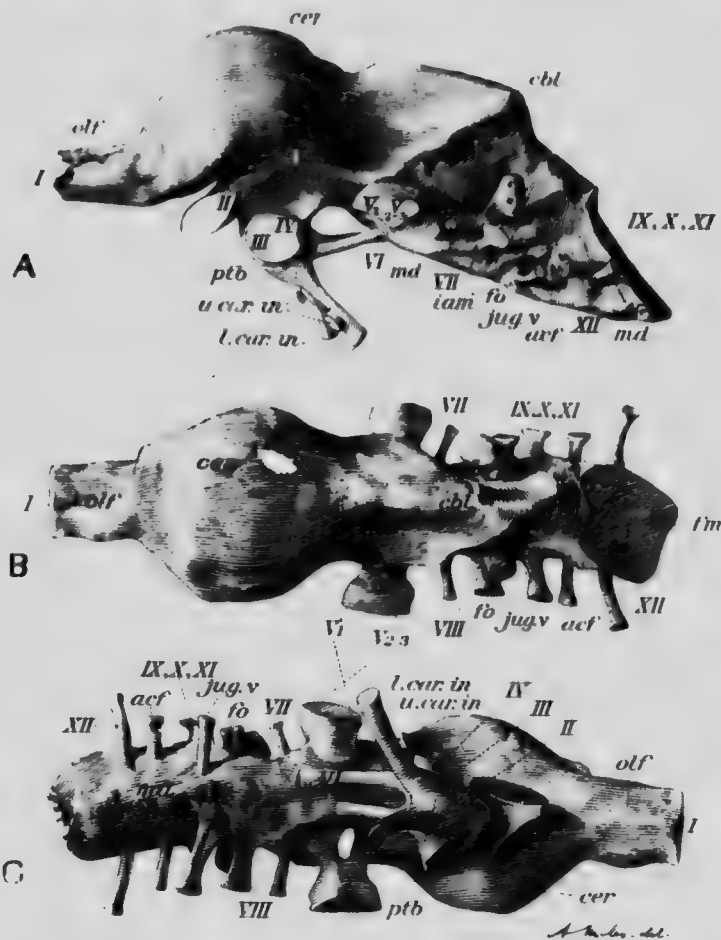


Figure 27. Cast of brain-cavity of *Edmontosaurus* (paratype, Cat. No. 2289);  $\frac{1}{3}$  nat. size. A, left lateral aspect; B, superior aspect; C, inferior aspect; *cbd*, cerebellum; *cer*, cerebrum; *l. car. in.*, lower entrance of internal carotid artery; *md*, medulla oblongata; *olf*, olfactory lobes; *opt*, optic lobe; *ptb*, pituitary body; *u. car. in.*, upper entrance of internal carotid artery; *I*, olfactory nerve; *II*, optic nerve; *III*, oculomotor nerve; *IV*, Pathetic or trochlear nerve; *V*, trigeminal nerve; *VI*, abducent nerve; *VII*, facial nerve; *VIII*, auditory nerve; *IX*, glossopharyngeal nerve; *X*, vagus or pneumogastric nerve; *XI*, spinal or accessory nerve; *XII*, hypoglossal nerve.

As seen from the side the upper outline descends rapidly in the front face of the cerebrum to the olfactory lobes where it continues horizontally forward. With the exception of the depression caused by the constriction behind the cerebrum, the superior outline, sloping gently forward, continues

back, but slightly lower in elevation than the cerebrum, to the cerebellum beyond which it has a rapid descent to the foramen magnum. The inferior outline ascends gradually from the floor of the foramen magnum to the forwardly placed pituitary body which depends in line with the posterior part of the cerebrum. The lower outline of the olfactory lobes is horizontal in advance of the backwardly ascending lower surface of the cerebrum.

Viewing the cast from above or below the greatest breadth is across the cerebrum in great contrast to the comparatively slender olfactory lobes, and the less slender but narrow portion extending back from the cerebrum.

The brain of *Edmontosaurus*, relying on the proportions of the cast of the brain-cavity, was about two and a half times as long as its maximum height, i.e., from the lower end of the pituitary body to the level of the upper surface of the cerebrum (cerebral hemispheres). For a little over half its length forward from the foramen magnum it is narrow, angulated above, and constricted on the sides over a considerable area above the auditory nerve. Forward it broadens greatly into the cerebrum and ends narrowly in the olfactory lobes. The cerebellum rising with a steep posterior slope, is laterally compressed, but does not reach as great an elevation as the cerebrum which is the highest part of the brain. The angulation of the upper surface continues forward from the cerebellum and ends at a constriction defining the hinder limit of the cerebrum. A lateral angulation runs obliquely downward and forward from the cerebellum to above the trigeminal nerve apparently marking the posterior boundary of the optic lobe. The constriction just mentioned (posterior commissure) is continued down the sides in advance of the optic lobe between it and the cerebrum (or behind the primary fore-brain or *tha'amen-cephalon* if it were recognizable).

The cerebrum is almost hemispherical in shape, broadly rounded in all directions above, and flatly convex transversely in its anterior surface which descends very rapidly to the olfactory lobes. Laterally where it reaches its greatest breadth it overhangs its flattened lower surface. The infundibulum extends downward in line with the posterior part of the cerebrum (from the primary fore-brain) narrowing below with a backward inclination and terminating in the pituitary body.

The olfactory lobes, not distinguishable as a pair in the cast, are produced horizontally forward and are together much broader than deep; they are transversely somewhat concave above and moderately convex below with a slight median, longitudinal angularity.

The medulla occupies about half the inferior length of the brain, and posteriorly is considerably higher than broad, angulated both above and below, with its greatest diameter at about midheight. Farther forward its sides are sunken, where the walls of the brain-case are thickened in the neighbourhood of the eighth nerve, and its lower surface becomes flattened, retaining, however, a slight transverse convexity.

*Measurements of Cast of Brain-cavity of Edmontosaurus (paratype, Cat. No. 2289).*

	Mm.
Length, posterior end of floor of foramen magnum to termination of optic lobes...	28.2
Breadth across cerebrum.....	7.7
Anterior height of olfactory lobes.....	15
Anterior breadth of olfactory lobes.....	3
Height vertically above lower end of pituitary body.....	5.5



Height in line with trigeminal nerve (V).....	74
Breadth at trigeminal nerve.....	54
Breadth just behind the facial nerve (VII).....	35
Height in line with auditory nerve (VIII).....	76
Breadth behind auditory nerve.....	42
Posterior height, from lower surface of medulla, in advance of hypoglossal nerve (XII).....	52
Posterior breadth at midheight of medulla.....	41

### Teeth.

Figure 28 shows the manner in which the teeth follow each other in the Hadrosauridae as a group. The number of vertical series in the dentary and maxillary magazines varies in the different generic forms as also does the number of individual teeth in the vertical series. The

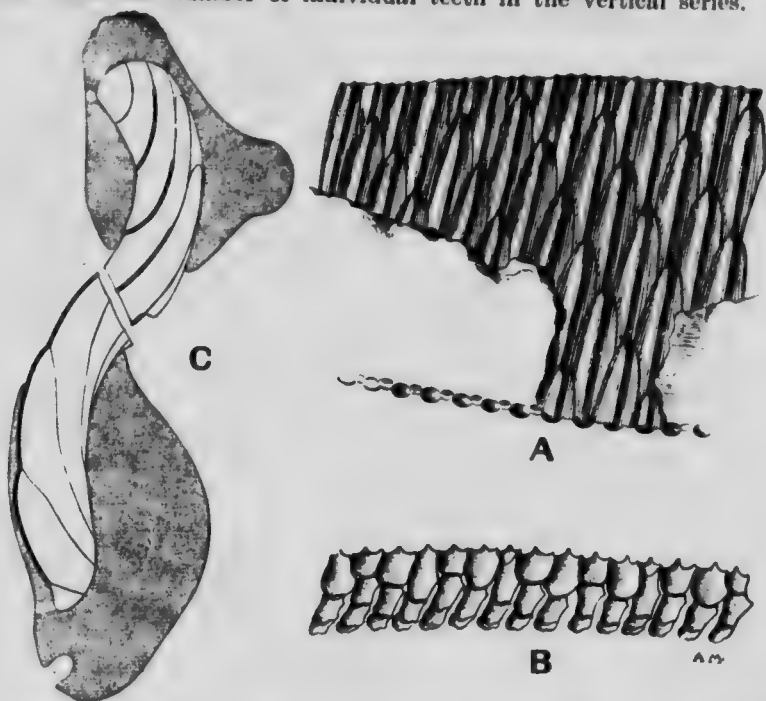


Figure 28. Illustrating the general type of tooth formation and succession in the Hadrosauridae. A, internal view of vertical series of teeth of lower jaw; B, view from above of teeth of lower jaw worn down by use; C, diagrammatic representation of teeth of both jaws in cross-section. † natural size.

large number of teeth in each jaw and their manner of implantation render the dentition remarkably complicated. As the teeth were evidently worn down rapidly a system of continuous replacement was necessary and for this purpose many reserve or successional teeth were provided in vertical series of from five to eight teeth, each tooth in a series overlapping the one which preceded it. The vertical series curved outward in the lower



jaw and inward in the upper one so that the worn surface of the teeth in the two jaws came together with a shearing action in an almost vertical direction. As a result of the curve in the vertical series, and of the overlapping of individual teeth therein, as many as three or even four teeth belonging to a series might be in use at the same time, viz., one worn down to a stump, and one, two, and sometimes three succeeding teeth in progressive stages of wear, providing a tessellated shearing surface of considerable breadth and having a length equal to that of the magazine. The dentary teeth succeed each other in both jaws from the inner side. In the dentary the enamelled face of the crown of the teeth is on the inside providing a continuous enamelled surface to the full extent of the magazine. The maxillary teeth bear enamel on their outer side and for this reason and in consequence of their inward curve the enamelled surfaces in the vertical series of teeth are not brought into juxtaposition after the manner of the mandibular teeth.

The teeth of *Edmontosaurus* conform to the general rules governing tooth implantation and succession in the Hadrosauridae and are arranged in the usual closely fitting vertical rows of which there are forty-eight or forty-nine in the dentary with four or five teeth and sometimes the stump of a sixth in each row.

The dentary teeth are largest at the mid-length of the magazine and decrease in size toward either end of it, the posterior ones being considerably shorter but only slightly narrower than those in front. The inner enamelled tooth-surfaces, in lateral aspect, are nearly lozenge-shaped in outline, with the longer diameter vertical, and fit closely together quincuncially in a mosaic which is almost half covered from below by the thin alveolar wall. The enamelled portion of the teeth is evenly rounded above, and emarginated at the narrow base where the apex of the next succeeding tooth closely fits. It bears a high, broad-based, sharp-edged, median keel running its length, between which and the margin on either side, the surface is evenly concave transversely. The succession of keeled teeth from below results in the whole of the inner face of the dentary magazine being regularly fluted in a vertical direction. A slight elevation of the margin is developed in the apical curve of the larger teeth, and is also present, to a varying extent, in the smaller anterior and posterior ones along the sides. In the majority of the dentary teeth the margins are smooth, but in the first five or six vertical rows marginal papillations occur between the tooth's apex and the angulation at its maximum breadth.

Three dentary teeth, of the same vertical series, in progressive stages of wear, are in use in the cutting surface at the same time. This number toward either end of the magazine is generally reduced to two.



Figure 29. Enamelled face of teeth, in twenty-ninth to thirty-first vertical series from the front, in left dentary of *Edmontosaurus*, Cat. No. 2289; natural size.

In the maxillary magazine there are from fifty-one to fifty-three vertical rows of teeth. The enamelled face of these teeth is narrower than that of the dentary, the median keel is higher in the upper or basal portion of the tooth, the margins toward the apex are more elevated, and, in the smaller teeth at either end, are crossed in an oblique direction by numerous papillose ridges. The outer enamelled faces of the teeth do not combine as on the inner side of the dentary magazine to form a continuous fluted surface but present a rather irregular, longitudinal row of crowns in which the less protrudent or non-functioning teeth are seen, where the roots of the used up teeth have dropped out, deep-set between the functioning ones. The maxillary teeth seem to have been, in the cutting surface, in a single, longitudinal row in successive sequences of three showing a progressive amount of wear. It is possible, however, that individuals of this genus, two maxillary teeth of the same vertical row, have been in the cutting surface near the mid-length of the jaw at the same time.

The cutting surface of the dentary magazine of teeth met that of the maxillary magazine in a shearing action after the manner of the blades of scissors. In many jaws of hadrosaurs these cutting tooth surfaces are set in an even plane longitudinally but are more or less undulatory as the result of unequal wear of individual teeth. For the same reason an unevenness of the surface in a transverse direction was frequent. The effectiveness of the jaws as shears was dependent on the evenness of the cutting surface of the dental magazines and the frequent occurrence of irregular curvature in these composite dental surfaces can be taken only as evidence of the inefficiency of this particular kind of dentition except for cutting and chopping the softest and most succulent of plants.

*Measurements of Teeth of Edmontosaurus, Cat. No. 2289.*

	Mm.
<i>Teeth of right dentary:</i>	
Non-functioning tooth of average size of those near the midlength of the magazine—	
Height of inner enamelled surface	34
Maximum breadth of same at midlength	11.5
Breadth at lower end of same	6
Non-functioning tooth from seventh vertical row from the front	
Height of enamelled surface	26
Breadth of same at midheight	10
Breadth of same at lower end	5
Non-functioning tooth from seventh vertical row from the back	
Height of enamelled surface	19
Breadth of same at midheight	9
Breadth of same at lower end	4
<i>Teeth of left maxillary:</i>	
Functioning tooth in twenty-fourth vertical row from the front—	
Height of outer enamelled surface	27
Breadth of same at midheight	8.5
Breadth of same at upper (basal) end	7
Functioning tooth in fifth vertical row from the front—	
Height of enamelled surface, about	17
Breadth of same at midheight	7
Functioning tooth in ninth vertical row from the back—	
Height of enamelled surface, about	17
Breadth of same at midheight	7

## VERTEBRÆ.

There are available for present description one cervical and three dorsal vertebrae belonging to the 1916 skeleton, Cat. No. 2289. In both skeletons the greater part of the tail is missing, in the type from behind the sixth caudal, in the paratype from behind the fifth, but in each the remainder of the vertebral column is apparently present. Until the enclosing matrix is removed the vertebral column as a whole cannot be described in detail, but the four vertebrae of the paratype so far taken from the rock supply with accuracy the characteristics of the majority of the presacral vertebrae, and indicate the changes in form and proportion that took place in passing back from the head.

There was a general increase in size in the presacral vertebrae in passing back in the series.

The cervicals, and the anterior dorsals at least, were strongly opisthocœlous. Neural spines were absent, or feebly developed in the majority of the cervicals until apparently late in the series. In the dorsals they were short anteriorly in the series but gained slightly in length posteriorly. The transverse processes in the anterior dorsals were long and stout, and pointed upward with an inclination outward and forward. In the posterior dorsals they were almost horizontal, and less robust. The cervical and dorsal ribs with the exception of the last dorsal, or possibly the last two or three, were double headed.

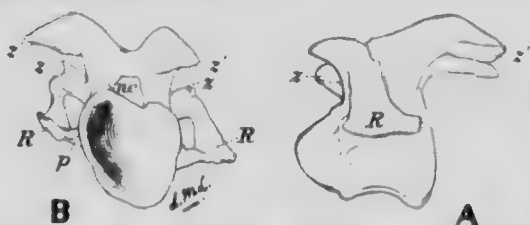


Figure 30. Cervical vertebra of paratype of *Edmontosaurus*, Cat. No. 2289;  $\frac{1}{2}$  natural size. A, left lateral view; B, posterior view. nc, neural canal; ns, neural spine; p, parapophysis; R, rib; tp, transverse process; z, prezygapophysis; z', postzygapophysis.

**Cervical Vertebra.** This vertebra (Figure 30) from the paratype of *Edmontosaurus* is apparently from near the middle of the cervical series. The centrum is deeply cupped behind, and the anterior end is correspondingly convex. It narrows to the front, and has a length considerably in excess of the posterior height and breadth which latter are

about equal. The ventral surface is narrow and flat, and angulated laterally where it passes into the excavated sides of the centrum. The anterior face is bounded posteriorly by a definite protruding girdle against which the narrow rim of the concave posterior end of the preceding centrum fitted. The neural arch is lower than broad enclosing a large neural canal. The transverse process is short and stout and is directed obliquely upward and outward horizontally in line with the neural canal; it terminates distally in a facet for the attachment of the tubercle of the rib, and gives off superiorly a short prezygapophysis. Laterally a short parapophysis with a narrow vertical diameter provides for the attachment of the head of the rib considerably below the level of the floor of the neural canal. The posterior zygapophyses are long, robust, and curve backward far beyond the posterior end of the centrum. The articulating surfaces of the post- and prezygapophyses facing downward and upward respectively, are

inclined but slightly from the horizontal. There is no neural spine. The neural arch ends in an angulation above from which two ridges diverge backward, one to each postzygapophysis. With this centrum both ribs are preserved to which reference will be made later.

*Measurements of Cervical Vertebra (distorted) of Paratype of Edmontosaurus.*

	Mm.
Maximum length, about.....	175
Maximum height, about.....	157
Length of centrum.....	123
Anterior height of same, about.....	74
Posterior height and breadth of same, about.....	85
Depth of concavity of posterior end of centrum.....	38
Diameter of neural canal.....	37

*Anterior Dorsal Vertebra.* The dorsal vertebra here described (Figure 31) is from the paratype of *Edmontosaurus* and is the anterior one of two having much the same size and proportions. It appears to be about the fourth or fifth from the front in the dorsal series. Two ribs, one of which is well preserved in its entirety (Figure 33), evidently belong, judging from their proportions, to this particular vertebra.

The centrum of this vertebra is opisthocœlous, but with the concavity and convexity less than in the cervical vertebra above described. It is longer than high, narrows downward, is pinched on the sides, and has a longitudinal keel below between the articulating ends. The neural arch is high and robust. The neural spine is short and does not rise much above the top of the transverse processes. It is broad in the fore-and-aft direction, inclined backward at an angle of about 45 degrees to the horizontal, is thin, and comes to a sharp edge along its anterior slope the base of which is vertically above the midlength of the centrum. It extends far beyond the posterior end of the centrum. It narrows slightly above its midheight, but regains its lower breadth by expanding above at the curved superior border which is thickened and rugose. The transverse processes are long and heavy, and rise upward at an angle of about 35 degrees to the vertical, inclining backward nearly as much as the neural spine. Anteriorly they come to a thin, sharp edge which is a continuation upward, with a change of direction outward of the narrow upper border of the prezygapophyses. Interno-posteriorly a thin flange is developed connecting them with the postzygapophyses. Externo-posteriorly a much stouter flange extends down to the posterior shoulder of the neural arch. Between these flanges a deep excavation leads downward and is separated from the corresponding excavation of the other side by a median lamella of bone extending up from the neural canal and supporting the pair of postzygapophyses from below.

The development of flanges in the transverse processes results in their being subtriangular in outline in cross-section. There is an inner face, broad and flat, an antero-external one becoming transversely concave in its upper part, and a third directed almost backward also concave with the concavity rapidly increasing below. The second and third faces are about equal in extent and both are narrower than the inner face.

The pre- and postzygapophyses, facing in opposite directions, are inclined at an angle of about 55 degrees to the horizontal, or about 70

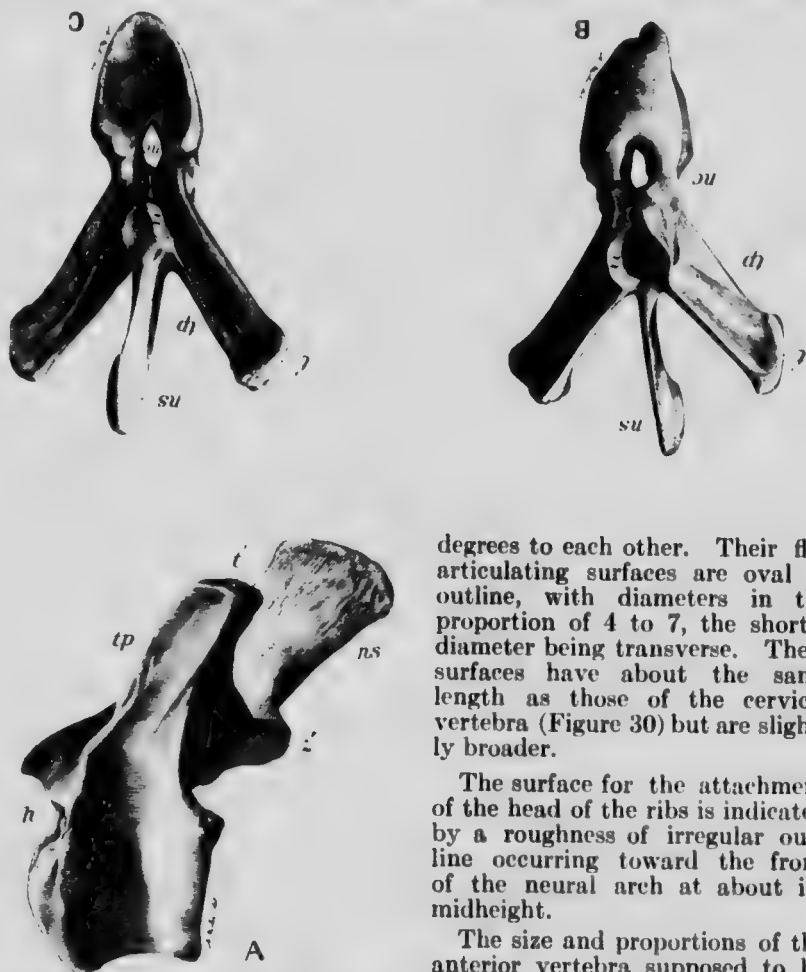


Figure 31. Anterior dorsal (?fifth) vertebra of *Edmontosaurus*, Cat. No. 2289;  $\frac{1}{4}$  natural size. A, left lateral aspect; B, anterior aspect; C, posterior aspect; *h*, surface for head of rib; *nc*, neural canal; *ns*, neural spine; *t*, surface for tubercle of rib; *tp*, transverse process; *z*, prezygapophysis; *z'*, postzygapophysis.

degrees to each other. Their flat articulating surfaces are oval in outline, with diameters in the proportion of 4 to 7, the shorter diameter being transverse. These surfaces have about the same length as those of the cervical vertebra (Figure 30) but are slightly broader.

The surface for the attachment of the head of the ribs is indicated by a roughness of irregular outline occurring toward the front of the neural arch at about its midheight.

The size and proportions of the anterior vertebra supposed to be the fifth or sixth of the series are very similar to the one above described and figured; it is equally well preserved and any special reference to it is not considered necessary.

*Measurements of Dorsal Vertebra (?fourth or fifth) of Paratype of Edmontosaurus.*

	Mm.
Maximum length.....	327
Maximum height.....	352
Length of centrum at midheight.....	151
Anterior height of centrum, about.....	97
Posterior height of same.....	93
Posterior breadth of same.....	81
Depth of concavity of posterior end of centrum.....	20
Height of neural canal, about.....	42
Anterior height of neural spine measured along its slope.....	194
Antero-posterior breadth of same at upper end.....	106
Transverse thickness of same at midheight.....	10
Length of transverse process measured from base of neural spine.....	128

*Posterior Dorsal Vertebra.* The vertebra shown in Figure 32 is apparently the last of the dorsal series judging from the small size of the single-headed ribs which are preserved attached to the transverse processes. This vertebra belongs to the paratype of *Edmontosaurus* and gives the changes in form that have resulted in passing to the back of the series. It has much the appearance of an anterior caudal vertebra which it might readily be mistaken for but for the presence of ribs. In comparison with the anterior dorsals there is an increase in size, the centrum is of a different shape, the neural spine is upright instead of sloping backward, and the transverse processes have become almost horizontal.

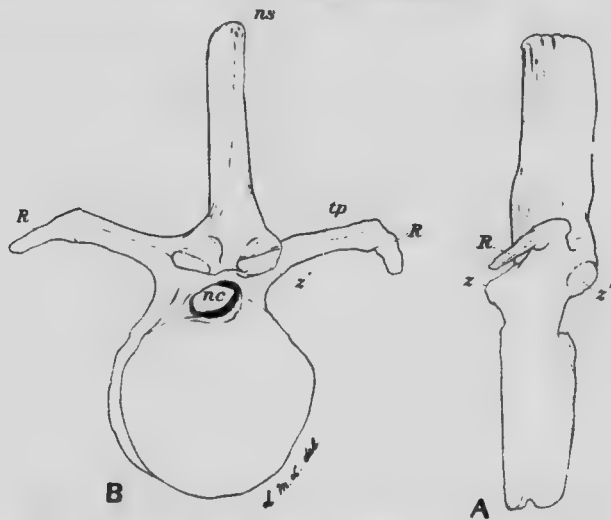


Figure 32. Posterior dorsal vertebra of paratype of *Edmontosaurus*;  $\frac{1}{2}$  natural size. A, left lateral aspect; B, posterior aspect. Lettering as in Figures 30 and 31.

The centrum is about as broad as high, and is very short. The posterior end is moderately concave, the anterior one almost flat with a slight convexity. The sides are deeply concave in a fore-and-aft direction, and ventrally a longitudinally directed ridge connects the two ends. In

comparison with the anterior dorsals the neural arch is lower, the neural spine longer, thicker, and not so broad antero-posteriorly.

The articulating surfaces of the zygapophyses are larger than in the anterior dorsals, the difference being principally in the breadth. Their outline is broadly oval, the proportion of breadth to length being about as 4 to 5. They slope at an angle of about 26 degrees to the horizontal and are farther apart than those of the anterior dorsals. The anterior border of the neural spine starts narrowly from between the prezygapophyses and is continued thinly upward to about the midheight of the spine. From each postzygapophysis a short, stout flange proceeds upward to the neural spine as lateral boundaries to a median excavation which becoming shallower in its upward course channels the posterior border of the neural spine to above its midlength.

The transverse processes are shorter than, and slender in comparison with, those of the anterior dorsals, and lack the latter's conspicuous development of flanges. They proceed directly outward from between the pre- and postzygapophyses with only a slight inclination upward. Their strongest connexion below is with the anterior border of the neural arch in the nature of a buttress merging with the prezygapophyses. The outline of their cross-section at midlength is somewhat oval with the greater diameter horizontal, more rounded in front than behind, and more than twice as broad as deep.

*Measurements of Posterior Dorsal Vertebra of Paratype of Edmontosaurus.*

	Mm.
Maximum height .....	498
Maximum breadth (distance between outer ends of transverse processes), about ...	317
Length of centrum .....	75
Breadth of same .....	184
Height of same .....	182
Amount of concavity of posterior end of same .....	25
Height of neural spine above base of transverse process .....	220
Antero-posterior breadth of same at midheight .....	74
Thickness of same at midheight .....	21
Height of neural canal .....	41

RIBS.

The ribs of *Edmontosaurus* at present available for description belong to the paratype and consist of the pair in place on the cervical vertebra above described (Figure 30), the pair preserved with the posterior dorsal also already described (Figure 32), and two, presumably a pair, apparently belonging to the anterior dorsal vertebra shown in Figure 31.

*Cervical Ribs.* The ribs of the cervical vertebra, Figure 30, are double-headed and very short, and consist mainly of a triangular plate of bone, diminishing backward, composed of the shaft and the broad tubercle set in a vertical plane. The neck is given off below from the front of and at right angles to the shaft, its junction with the shaft being sharply angulated externally. The neck is broad antero-posteriorly, and thin, thickening internally for the formation of the head. This latter, connecting with the short parapophysis, is much broader antero-posteriorly, than deep. The posterior portion of the shaft is short, slender, and triangular in cross-section, being flat above, and keeled below by the backward continuation of the angulation at the outer termination of the neck.

**Thoracic Ribs.** Of the pair of ribs assigned to the anterior dorsal vertebra (?fourth or fifth) the one of the right side is complete and well preserved, the left one is in an equally good state of preservation but lacks a short piece from the lower end.



Figure 33. Right rib of ?fourth or fifth dorsal vertebra of paratype of *Edmontosaurus*; anterior view obliquely from without;  $\frac{1}{2}$  natural size. h, head; t, tubercle.

These anterior ribs (Figure 33) are long and strongly built with a moderately curved, tapering body or shaft, a well-developed head and tubercle, and a deep, thin neck. In the upper half of the shaft the bone is thick with a rounded border along the antero-internal curve and down to the head; along the postero-external curve and between the tubercle and the head it comes to a rather thin edge. The broadest part of the rib is below the tubercle. The posterior face in the upper half of the shaft, and for a short distance past the tubercle toward the inner border of the neck, is transversely concave. For a corresponding distance on the anterior face the surface is transversely convex, the convexity developing down the shaft into a well-defined median ridge which merges farther down into the antero-internal border. It is along this ridge that the bone is thickest. In the lower half of the shaft the bone becomes more nearly oval in cross-section being somewhat thicker near the outer curve with the greatest diameter directed externo-internally. Along this lower portion of the shaft the rate of taper is lessened. At the extreme lower end the bone thickens and there is a roughened surface for the attachment of the costal cartilage. The neck is directed downward, inward, and slightly forward at an angle of about 110 degrees to the upper part of the shaft.

The head of the rib is set rather squarely across the neck and expands to a thickness which is twice that of the neck near its lower border. Its articular surface is undulating, pitted, and rugose with an irregular lengthened oval outline about twice as deep as broad.

The tubercle is prominent but much smaller than the head. Its articular surface is about half that of the head in area and is set at much the same angle. From the point of view at which the rib has been drawn neither of these articulating surfaces is fully seen in Figure 33.



*Measurements of Right Thoracic Rib (?fourth or fifth) of Paratype of Edmontosaurus.*

	Mm.
Length along antero-internal curve from the head to the lower end (about 53½ inches).....	1,360
Distance from upper end of tubercular facet to top of head.....	180
Depth from top of tubercle to inner curve.....	140
Depth of neck at about its midlength.....	75
Thickness near lower border of same.....	17
Height of capitular facet.....	74
Breadth of same.....	35
Height of tubercular facet.....	45
Breadth of same.....	28
Greater diameter of lower extremity.....	41
Lesser diameter of same.....	24
Greater diameter of rib at midlength.....	42
Lesser diameter at midlength.....	21

The ribs attached to the large posterior dorsal vertebra (Figure 32) are very short with a length of only about 85 mm. They decrease in diameter rapidly for one-third of their length outward from the transverse process and then retain much the same size for the remainder of their length. They are vertically compressed with the greater diameter equal to about twice the lesser one. They incline a little forward and have the upper surface directed slightly to the front.

*Fore Limb.*

*Humerus.* The humerus of *Edmontosaurus* is a robust bone slightly over four times as long as its upper transverse breadth. The radial crest is very strongly developed and is the most conspicuous feature of the bone giving to it in its upper half the great breadth common to the humeri of the Hadrosauridæ.

In the right humerus, Figure 34, of the paratype of *Edmontosaurus*, the shaft is somewhat sigmoid in its length bending backward in its upper half and to about the same extent forward below. The head is rather small and occupies a central posterior position superiorly overhanging the shaft. It is supported beneath by a strong buttress, with a rounded border, passing below into the posterior face of the shaft. It is roughened on the upper and hinder portions of its convexity, is deeper than broad, and forms the highest part of the upper surface of the bone. The inner and outer tuberosities extend outward on either side of, and at a lower level than, the head with a forward curvature which renders the anterior face of the bone above concave. Of the two tuberosities the internal one is the stouter. The radial crest extends downward on the shaft from the outer tuberosity as a comparatively thin flange to below the midheight of the bone. It keeps about the same breadth downward before it suddenly narrows and becoming increasingly thicker merges into the shaft. From the inner tuberosity an obtusely angulated ridge extends down the shaft with decreasing prominence to below the level of the radial crest. The shaft below the radial crest is thick and strong with a somewhat ovate outline in cross-section, the greatest thickness being anterior and slightly external. The lower extremity narrows slightly backward and is flattened on the sides. The condyles are well rounded below, narrow transversely,

and protrudent in front. The inner one is the larger of the two and thicker both in front and behind. Its fore-and-aft diameter is equal to the maximum combined condylar breadth. The condyles are separated below by a deep groove which behind continues up between them to the shaft and in front widens into a large concavity. Posteriorly on the shaft, toward the inner side, at about one-third of the bone's length from the top, there

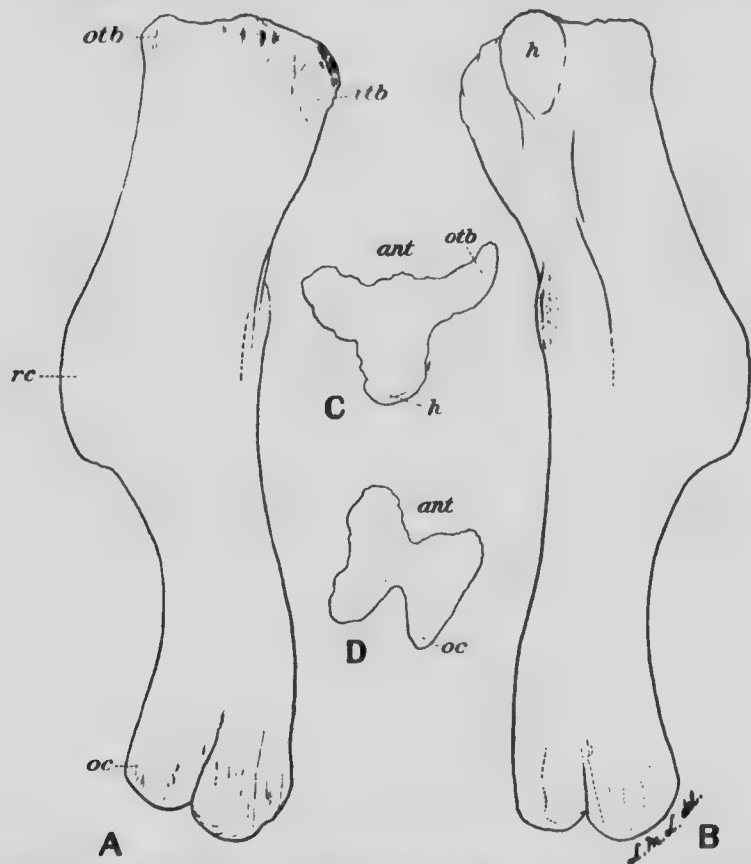


Figure 34. Right humerus of paratype of *Edmontosaurus*;  $\frac{1}{2}$  natural size. A, anterior aspect; B, posterior aspect; C, outline of proximal end; D, outline of distal end; *ant*, anterior; *h*, head; *itb*, inner tuberosity; *oc*, outer condyle; *oth*, outer tuberosity; *rc*, radial (deltoid) crest.

is a prominent, roughened, vertical ridge for muscular attachment. Also the lateral surfaces of the distal end of the bone, and the border, and external face, of the radial crest in its lower part are coarsely striated for muscles. As the radial crest is directed obliquely outward and forward it is foreshortened when viewed as in Figure 34, A and B, and appears narrower than it really is.

*Measurements of Right Humerus of Edmontosaurus, Cat. No. 2289.*

	Mm.
Length.....	694
Maximum transverse breadth at proximal end.....	167
Distance from lower angulation of radial crest to posterior face of shaft.....	165
Thickness of radial crest at its midlength and breadth.....	21
Thickness of same at a short distance in from its lower angulation.....	36
Antero-posterior diameter of shaft at one-third of the bone's length from distal end.....	92
Interno-external diameter at same level.....	70
Maximum transverse breadth of distal end.....	116
Antero-posterior diameter of inner condyle.....	114
Antero-posterior diameter of outer condyle.....	104

*Ulna (U).* Figure 35. The ulna is the longest bone of the fore limb, the humerus being the next in length, with the radius slightly shorter than the humerus. The ulna exceeds the radius in length by about 95 mm. It is slender for its length, is heaviest in its upper half, and reaches its maximum size proximally. Distally it is only slightly enlarged. At its upper end its outline in cross-section is triangular. Here the olecranon process is well developed rising to a considerable height above the articular surface for the humerus. Anteriorly toward the inner side above it is excavated for the proximal end of the radius, the excavation narrowing and lessening downward, and disappearing above the bone's half-length. Below the olecranon process posteriorly there is a protrudent angulation which accentuates the general forward bend of the bone in its upper part. At midheight the shaft is oval in cross-section, with the greater diameter fore-and-aft, and one and a half times the lesser diameter. Distally the greatest diameter is nearly twice the maximum transverse breadth, and on the inner side toward the front there is a rugosely striated, depressed surface for the close application of the distal end of the radius. Throughout, the lower end of the ulna is deeply striated in a longitudinal direction for the insertion of muscles.

*Measurements of Left Ulna of Paratype of Edmontosaurus.*

	Mm.
Length.....	760
Maximum transverse breadth of proximal end.....	128
Maximum diameter of distal end.....	114
Maximum diameter at midlength.....	80

*Radius (Ra).* The radius, Figure 35, is slender, nearly straight, and shorter than the ulna, with a length equal to about  $6\frac{1}{2}$  times its

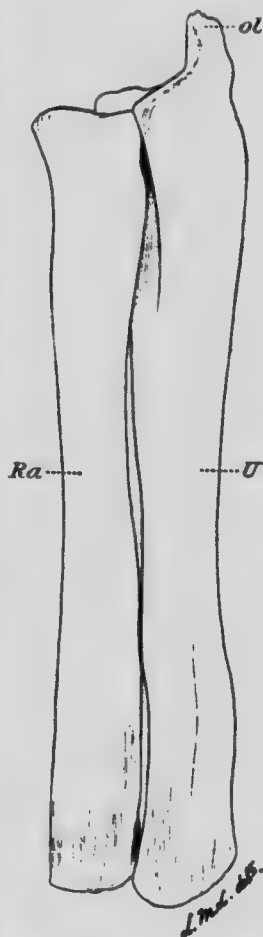


Figure 35. Left ulna and radius of paratype of *Edmontosaurus*;  $\frac{1}{2}$  natural size; anterior view slightly from without. *ol*, olecranon process; *Ra*, radius; *U*, ulna.

maximum thickness proximally. Both ends are enlarged, the proximal one more than the distal one. In comparison with the ulna, the radius is more slender throughout, with less disparity in the size of the ends. At midheight the shaft has an elliptical outline in cross-section as in the ulna but smaller, the diameters in the two bones being in about the proportion of 4 to 5. The outline of the proximal end in superior aspect is nearly square with the greater diameter transverse and the outer and posterior sides fitting into the angular excavation of the ulna. The increase in the size of the proximal end is rapid on the inner and hinder faces, particularly on the latter. Externo-anteriorly for some distance below the upper end the bone narrows outwardly forming a vertical ridge, most protrudent above, which is rugosely striated in the direction of its length and is in close contact, when the bone is in position, with the ulna. The lower end is angulated internally and thickens toward the outer side where it is applied to the ulna. On all sides it is longitudinally striated deeply for muscular attachment. Similar striations are conspicuous also at the upper end.

*Measurements of Left Radius of Paratype of Edmontosaurus.*

	Mm.
Length.....	65
Maximum transverse breadth of proximal end.....	98
Maximum diameter of distal end.....	87
Maximum diameter at midlength.....	65

### THE GENUS EDMONTOSAURUS.

The orthopod genus *Edmontosaurus* of the family *Hadrosauridae*, subfamily *Hadrosaurinae* (p. 68) represented by the single species *E. regalis*, Lambe, has the following characters:

*Generic and Specific Characters.* Skull moderately elongate, high and broad posteriorly, flat in the frontal region, laterally compressed behind a low, greatly expanded snout. Orbit large. A large pocket-like recess developed within the postfrontal, leading from the orbit. Lateral temporal fossa restricted above. Palatine and pterygoid rising, at a high angle, inward. Ectopterygoid external to the maxillary and pterygoid, connecting the two. Mandible deep and strong, very slightly decurved in front. Teeth with a rounded apical outline in lateral aspect, keeled, and with smooth borders; in 48-49 vertical rows in the dentary, and 51-53 in the maxillary. Ischium long, bluntly pointed distally. Femur slightly longer than the tibia. Humerus nearly as long as the ulna. Cervical and dorsal vertebræ opisthocœlous, in a marked degree in the former. Dorsal spines of moderate size, increasing slightly in height backward in the series. Sacrum composed of eight vertebræ. Animal of robust build, between 30 and 40 feet long.

*Edmontosaurus* approaches most closely *Diclonius* Cope of later geological age, one of the principal characters distinguishing the two being found in the general shape of the skull which in *Edmontosaurus* is high and in *Diclonius* greatly depressed. The name *Diclonius*, as used here, is reserved for *D. mirabilis*, Cope, from the Lance formation of Dakota, sometimes referred to as *Trachodon mirabilis* a genus and species insecurely established by Leidy in 1856, on the tooth from the Judith River beds of

Montana. No characters can at present be assigned to *Trachodon* beyond those derived from the single mandibular tooth which constitutes the type.<sup>1</sup>

*Edmontosaurus* rivalled in size its bulky contemporary *Hypacrosaurus*. It appears, however, not to have been as large as *Prosaurolophus*, from the Belly River formation of Alberta, if the skull in the *Hadrosauridæ* can be considered a criterion of the size of the animal as a whole.

## CLASSIFICATION OF THE HADROSAURIDÆ.

### DIVISION INTO THREE SUBFAMILIES.

The discovery in recent years of many new generic forms of *Hadrosauridæ* in the western Cretaceous of this continent, more especially in the Belly River and Edmonton formations of Alberta, has greatly enlarged the list of known genera of these herbivorous dinosaurs, and has been the means of increasing our knowledge of their osteology. As a result of the study of these forms it is apparent that three principal groups or subfamilies are represented.

In 1914<sup>2</sup> a classification of the *Hadrosauridæ* (*Trachodontidæ*) was proposed by Mr. Barnum Brown who recognized two subfamilies, viz., the *Trachodontinæ* and the *Saurolophinæ*. Since then, principally through the discovery (1915) and further study of *Cheneosaurus*, the discovery in 1917 of a nearly perfect skull of *Stephanosaurus*, and the additional study of the family as a whole, greatly assisted by the well-preserved specimens in the collections of the Geological Survey, it has become evident that certain forms included in the *Saurolophinæ* differ from the *Saurolophus* type in so many fundamental particulars that their withdrawal to form a new subfamily is necessary. For this third subfamily of the *Hadrosauridæ* the name *Stephanosaurinæ* is proposed, to include the genera *Stephanosaurus* Lambe, *Corythosaurus* Brown, *Cheneosaurus* Lambe, and probably *Hypacrosaurus* Brown. Under the proposed new classification the *Saurolophinæ* are represented by *Prosaurolophus* Brown, and *Saurolophus* Brown. The *Hadrosaurinæ* (*Trachodontinæ* Brown) embrace *Gryposaurus* Lambe, *Kritosaurus* Brown, *Edmontosaurus* Lambe, "*Claosaurus*" Marsh, and *Diclonius* Cope.

The characters denoting the resemblances and dissimilarities of the three subfamilies, as provided principally by the skull, are as follows:

<sup>1</sup>"On the genus *Trachodon* of Leidy," by L. M. Lambe, *Ottawa Naturalist*, vol. XXXI, No. 11, February, 1918.

<sup>2</sup>*Bull. Am. Mus. Nat. Hist.*, New York, U.S.A., vol. XXXIII, art. XXXV.

*Hadrosauridae.*

Subfamily <i>Hadrosaurinae</i>	Subfamily <i>Saurolophinae</i>	Subfamily <i>Stephanosaurinae</i>
Forms large. Posterior height of skull variable. Supraorbital region flat. Fronto-parietal area enlarged. Nasals extending far forward. Anterior nares transversely confluent. Nasal passages anteriorly not enclosed in bone.  Premaxillaries confined to an anterior position.  Lachrymal of moderate size. Ischium pointed distally. Genera: <i>Gryposaurus</i> . Belly River formation. <i>Kritosaurus</i> . Ojo Alamo beds of New Mexico = ? <i>Edmonton</i> formation. <i>Edmontosaurus</i> . Edmonton formation. "C <sup>1</sup> <i>laosaurus</i> ". Lance formation. <i>Diclonius</i> . Lance formation.	Forms large. Skull high posteriorly. Supraorbital crest developed. Fronto-parietal area moderately large. Nasals extending far forward. Anterior nares transversely confluent. Nasal passages anteriorly not enclosed in bone.  Premaxillaries confined to an anterior position.  Lachrymal large. Ischium expanded distally. Genera: <i>Prosaurolophus</i> . Belly River formation. <i>Saurolophus</i> . Edmonton formation.	Forms of variable size. Skull high: relatively short. Supraorbital region elevated into hood, or dome. Fronto-parietal area reduced. Nasals retracted. Anterior nares separated by premaxillaries. Nasal passages enclosed by premaxillaries, and greatly enlarged in supraorbital region. Premaxillaries prolonged backward and entering largely into formation of hood or dome. Lachrymal reduced. Ischium expanded distally. Genera: <i>Stephanosaurus</i> . Belly River formation. <i>Corythosaurus</i> . Belly River formation.  <i>Cheneosaurus</i> . Edmonton formation. ? <i>Hypacrosaurus</i> . Edmonton formation.

From the above comparison of the subfamilies of the *Hadrosauridae* it is apparent that the *Hadrosaurinae* and the *Saurolophinae* show a closer approach to each other than to the *Stephanosaurinae*. These last stand apart with very marked and striking characteristics in about an equal degree from both the others. In them there is a supraorbital enlargement of the skull due to the surprisingly great development and backward extension of the premaxillaries and nasals. In the *Saurolophinae* instead of a general superior enlargement of the skull there is a crest over the eyes, formed by the nasals in *Prosaurolophus*, and, according to Brown, by the nasals, prefrontals, and frontals in *Saurolophus*.

The only one of the above listed characters common to the *Saurolophinae* and the *Stephanosaurinae* is the distal expansion of the ischium. It was this "footed" form of ischium, discovered by the writer in 1898, and first described by him in 1902<sup>1</sup>, in connexion with his original description of *Trachodon* (*Stephanosaurus*) *marginatus*, and not until then known in association with any type of orthopod (predentate) dinosaur, that was considered by Hatcher to belong to "some member of the Theropoda"

<sup>1</sup>Contributions to Canadian Paleontology, vol. III (quarto), pt. II.

as expressed in his "Geology and palaeontology of the Judith River beds," 1905, p. 97.<sup>1</sup> This author in the writer's opinion also erred in his remarks<sup>2</sup>, under the same heading in his report, on the material on which *S. marginatus* was established, as further work on the rich dinosaurian fauna of the Belly River beds of Alberta has so fully proved.

The members of the *Hadrosaurinae* and *Sauropophinae* resemble each other in having an elongated narial vacuity, opening through the skull, enclosed above by the nasals and premaxillaries. In both subfamilies there is a forward extension of the nasals, and a limitation of the premaxillaries to an anterior position in the skull. They differ from each other in the absence in the first and the presence in the other of a "foot" or distal expansion in the ischium.

The three subfamilies show distinctive characters in the relative size of the parieto-frontal region, and of the lachrymal.

The *Stephanosaurinae* are characterized by an extremely high skull in marked contrast to the relatively low skull of the *Hadrosaurinae* and *Sauropophinae*, the extreme of skull depression being reached in the *Hadrosaurinae*, viz., in the genus *Diclonius*. The primary character<sup>3</sup> of the *Stephanosaurinae* separating it from the other two are—(1) the envelopment of the anterior nares in, and their separation by, the premaxillaries (2) the extreme backward extension of the premaxillaries and their enclosure of the narial passages, (3) the enlargement of each narial passage posteriorly, within the supraorbital hood or dome, into an extensive air-chamber bounded by the premaxillaries and nasals.

In these subfamilies the appendicular skeleton and that of the trunk provide also characters which no doubt can be relied on as being distinctive in each.

The *Stephanosaurinae* were more highly specialized than either the *Hadrosaurinae* or the *Sauropophinae*. The arrangement of the elements enclosing the anterior nares and narial passages implies different habits and may indicate a better adaptation to an aquatic life.

The earliest member of the *Hadrosaurinae* is *Gryposaurus* from the Belly River formation of Alberta represented in Figure 36A by the skull of *G. notabilis* remarkable for its completeness and wonderful state of preservation.

The second genus of this subfamily, viz., *Kritosaurus*, from a not definitely determined geological horizon in New Mexico (the Ojo Alamo beds of San Juan county—?Edmonton formation of Alberta) is noteworthy for the great posterior height of the skull. The radical differences between *Gryposaurus* and *Kritosaurus*, particularly those conspicuously seen in the shape and size of the prementary and the proportionate length of the quadrate, make it probable that further fundamental dissimilarities will be revealed in the skull and other parts of the skeleton when the osteology of *Kritosaurus* is better known.

The type of *Kritosaurus* consists in general terms of the hinder half of the cranium, and a complete mandible, which latter reveals the length of the skull (Figure 36B). The orbital rim, including the postorbital bar, is, in the mounted skull, mostly restored in plaster, and all the facial

<sup>1</sup>"Geology and palaeontology of the Judith River beds", by T. W. Stanton and J. B. Hatcher, with a chapter on the fossil plants by F. H. Knowlton; Bull. No. 257, U.S. Geol. Surv.

<sup>2</sup>Cited by C. F. Bowen in "The stratigraphy of the Montana group, with special reference to the position and age of the Judith River formation in north-central Montana", Prof. Paper 90, U.S. Geol. Surv., 1914.

elements in advance of the orbit, with the exception of the maxillary, have also been restored, providing a rather remarkable nasal and pre-maxillary contour. The maxillary appears to be preserved to near its lower anterior extremity.



Figure 36. Skulls of Hadrosaurinae. A, *Gryposaurus*, Lambe; B, *Kritosaurus*, Brown.  $\frac{1}{2}$  natural size.

*Edmontosaurus*, "*Claosaurus*" *annectens*, and *Diclonius*, Figures 37C, D, and E, respectively, the remaining members of the *Hadrosaurinae*, illustrate well the general tendency in the crestless forms to a lowering of the skull as time progressed.



Figure 38F is of a skull of *Prosaurolophus maximus* Brown, obtained by C. M. Sternberg of the Geological Survey vertebrate palaeontological party of 1914 from beds of the Belly River formation on Red Deer river,



Figure 37. Skulls of Hadrosaurinae. C, *Edmontosaurus*, Lambe; D, "*Claosaurus*," Marsh; E, *Diclonius*, Cope.  $\pm$  natural size.

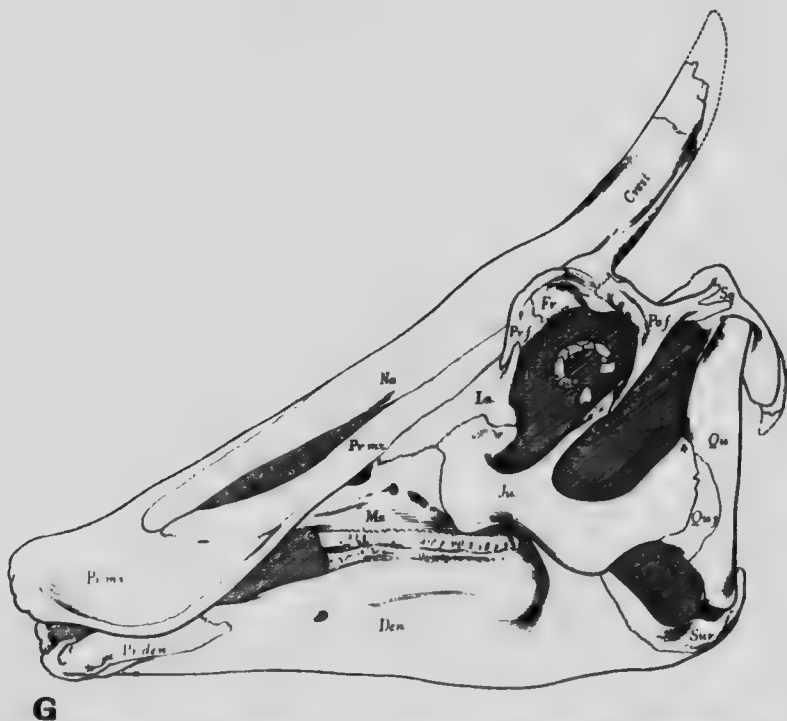
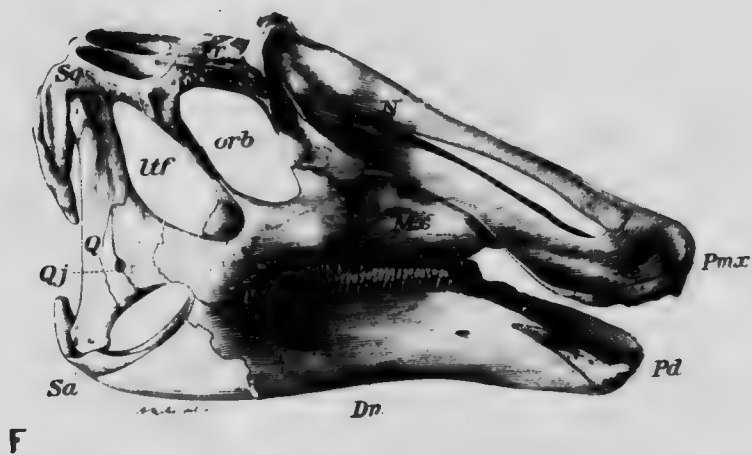


Figure 38. Skulls of Saurolophinae. F, *Prosaurolophus*, Brown; G, *Saurolophus*, Brown, ★ natural size.

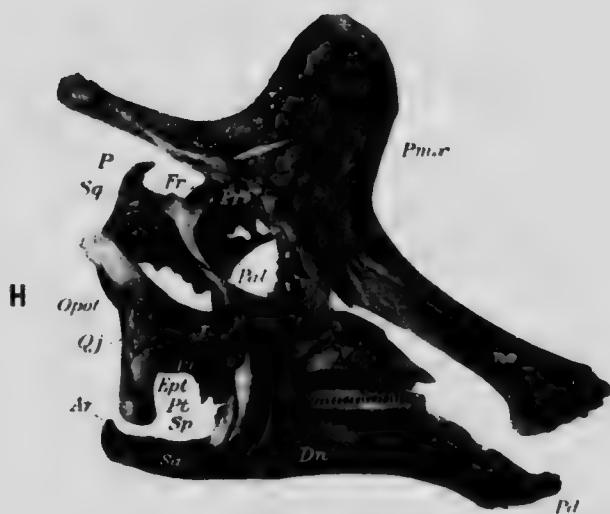


Figure 39. Skulls of Stephanosaurinae. H, *Stephanosaurus*, Lambe; I, *Corythosaurus*, Brown; J, *Cheneosaurus*, Lambe.  $\frac{1}{2}$  natural size.

2 miles east of the mouth of Little Sandhill creek. The specimen consists of all the cranium and mandible in advance of a line passing irregularly down from the front end of the supratemporal fossæ, and supplies the shape of the mandible, and the true length of the snout which is apparently restored to too great a length in the genotype described by Brown in 1916.<sup>1</sup> In the Geological Survey skull the premaxillary and nasal bones are complete and give the proper extent and manner of union of the nasal anteriorly with the upper limb of the premaxillary, the true outline of the posterior termination of the lower limb of the premaxillary, and the position and shape of the posterior end of the nasals. Both the upper and lower teeth are well preserved. The specimen proves that in *Prosaurolophus* the "crest" is formed entirely from the nasals and not chiefly from the frontals as supposed by Brown. In Figure 38F the posterior end of the skull is restored from Brown's figure of the genotype. The skull of *Prosaurolophus* is thus seen to be much shorter than originally described and more in accord with the outline of *Saurolophus* Brown, from the Edmonton formation.

A great advance was made in our knowledge of the structure of the skull of *Stephanosaurus* by the discovery in 1917 in the Belly River formation, Red Deer river, of a skull of *S. marginatus* much more complete and better preserved than the one described by the writer in 1914.<sup>2</sup> In the 1917 specimen (Figure 39H) the extraordinary contour of the head is fully given, and as most of the sutures are traceable, the boundaries of the various elements are revealed, clearing up points of doubt as regards the determination of the bones not only in *Stephanosaurus* but also in *Corythosaurus* and *Cheneosaurus*, other known members of the subfamily.

In the *Stephanosaurinae* the premaxillaries are greatly extended and enlarged posteriorly relegating the nasals to a position surprisingly far back in the skull.

In *Stephanosaurus* the top of the skull bears a high hood or crest, narrow from front to back, and laterally compressed, from whose posterior base there is a comparatively slender backward prolongation forming a process which reaches far beyond the occiput at a considerable distance above the level of the parieto-squamosal bar. The crest with its posterior extension is made up of the premaxillary and nasal bones. The inferior portion of the premaxillaries is greatly expanded posteriorly to form the central, lower part of the crest proper on either side. Superiorly the premaxillaries form the whole of the crest above, rising vertically in front and descending as steeply behind, thence continuing backward to take part in the formation of the posterior process. The nasals extend obliquely upward and forward from in advance of the small frontals and appear externally in the crest between the broad hinder termination of the inferior part of the premaxillaries (which cannot properly be referred to as a *lower limb* of the premaxillary) and the posterior descending portion of the premaxillaries above. They also extend narrowly backward beyond the frontals as part of the crest prolongation constituting the lower surface of the process, embracing the premaxillaries from below, and more posteriorly enveloping them externally also. In the back part of the crest, therefore, and in the crest-prolongation, the premaxillaries are between

<sup>1</sup>Bull. Am. Mus. Nat. Hist., vol. XXXV, pp. 701-708, figs 1 and 3.

<sup>2</sup>The Ottawa Naturalist, vol. XXVIII, pp. 17-20, plate I.

the nasals, that is along the whole of the latter's length. A long, narrow vacuity in the crest occurs between the nasals and the lower premaxillary expansion.

A broad, shallow groove runs obliquely upward and slightly backward across the lower portion of the premaxillary a short distance in advance of the anterior end of the jugal. This groove was considered to mark the back termination of the lower part of the premaxillary ("lower limb of the premaxilla") in the original description of the skull of *Stephanosaurus*. What was then named prefrontal is now clearly seen to be the greatly expanded postero-inferior part of the premaxillary as the structure of the bone is continuous across the groove. The prefrontal is small and assists in the formation of the orbital rim between the lachrymal and the postfrontal. The small frontal is excluded from the orbital rim by the prefrontal and postfrontal, and is well under the anterior, lower surface of the naso-premaxillary process.

In the light of our increased knowledge of the structure of the skull of *Stephanosaurus* the original description of the skull of *Corythosaurus* Brown can be amended in certain particulars. What was called prefrontal (Figure 39H) is now clearly seen to be premaxillary. The bone above the orbit determined by Brown as frontal is prefrontal. The frontal is small, as in *Stephanosaurus*, and is hidden beneath the crest. What is named frontal above the postfrontal and squamosal and forming the lower, hinder border of the crest is nasal. The front part of the crest is not nasal but the prolongation upward of the premaxillary. If the suture in the anterior part of the crest in Brown's figure of *Corythosaurus*, marking the back termination of the nasal (premaxillary) be correct then the whole of the crest above the narrow central vacuity may be nasal. If this line be not a suture then the premaxillaries form the upper part of the crest somewhat as in *Stephanosaurus*.

In the *Stephanosaurinae* the premaxillaries separate the external nares and nasal passages, the latter being enclosed outwardly by an upward growth of the floor of the passage and a downward bend of the roof of the same.

In *Stephanosaurus* the nasal passages lead up into the front part of a large double chamber within the crest, the entry being made at about the midheight of the chamber on either side of a vertical median septum. This nasal chamber occupies the greater part of the crest within, is flanked outwardly by the premaxillary and nasal bones and is somewhat over 150 mm. in height, and narrow from side to side, with a fore-and-aft diameter about three-fifths the height. An exit from the chamber is present below posteriorly leading downward. The position of the chamber is indicated externally by the greater convexity of the crest laterally in an area surrounding the narrow central vacuity. The *Stephanosaurinid* form of the external nares of *Corythosaurus* and *Cheneosaurus* point to the presence of a nasal chamber in these genera also.

It may be stated here that the determination of the nasal bone in *Stephanosaurus* rests not only on the evidence of the skull shown in Figure 39H, but also on that of fragmentary *stephanosaurinid* crania in which the sutural surfaces for the nasals are preserved in complete frontals.

In the brain-case of the skull of *Stephanosaurus* (Figure 39H) the sutures can be readily traced between the presphenoid and orbitosph<sup>enoid</sup>, and between the orbitosph<sup>enoid</sup> and alisphenoid. Also the suture between

the alisphenoid and the basisphenoid is preserved, proving by its position that the large flange, directed outward from above and somewhat behind the basisphenoid process, belongs to and is part of the basisphenoid. It may be of interest also to note that in this skull the ophthalmic branch of the trigeminal nerve (V) is enclosed in bone in its forward course and does not occupy an open channel as it appears to do in *Edmontosaurus*. Further, indicating an unusually perfect preservation of structural detail, the separation of the fenestra rotunda from the fenestra ovalis by a horizontal bar of bone is excellently shown.

To the preparation of this skull by C. M. Sternberg, its discoverer in the field, are due many details of structure that less skilful and painstaking work would not have revealed.

With a better understanding of the stegosaurinid skull certain errors in the description of the skull of *Cheneosaurus* (Figure 39J) as it appeared in the pages of the *Ottawa Naturalist* in 1917, can now be rectified. What was regarded as prefrontal is certainly the expanded prolongation backward of the lower, external part of the premaxilla, and the supposed sutural line running forward from the lower end of the lachrymal (see original figure) is evidently a fracture in the bone. The convex, upper surface of the dome is nasal met in front by the upper part of the premaxillary roofing the nasal passage. The bone above the orbit called supraorbital in the first instance is the prefrontal, and the frontal is similar to the frontal in both *Stephanosaurus* and *Corythosaurus* in being small and excluded from the orbital rim by the intervention of the prefrontal and postfrontal.

The posterior height of the skull shows a marked difference in five genera of crestless or flat-headed hadrosaurs (*Hadrosaurinae*) from the Cretaceous of the west of this continent, viz., in *Kritosaurus* (horizon uncertain = ?Edmonton formation), in *Edmontosaurus* (Edmonton formation), in *Gryposaurus* (Belly River formation), and in "*Claosaurus*" (*annectens*) and *Diclonius* both from the Lance formation. In *Kritosaurus* Brown, from the Ojo Alamo beds of New Mexico, the quadrate is of remarkable length, in *Diclonius* Cope, from Dakota, it is singularly short, the two representing the extremes of skull elevation and depression in the *Hadrosaurinae* (*Trachodontinae* of Brown). In these five genera, in all of which, with the exception of *Kritosaurus*, the skull is fully known from excellent material, the proportionate lengths of the quadrate and skull may be expressed in numbers as follows: *Kritosaurus* 1—over 2; *Gryposaurus* 1—2½; *Edmontosaurus* 1—over 2½; "*Claosaurus*" 1—nearly 3; and *Diclonius* 1—nearly 4. From this comparison it is seen that in *Kritosaurus* the posterior height of the skull (length of quadrate) relative to the horizontal length of the same is the greatest, that *Kritosaurus*, *Gryposaurus*, *Edmontosaurus*, and "*Claosaurus*" form a series, in the order named, in which the quadrate is successively reduced in length in about the same ratio, and that the greatest difference in the height of the skull is found between "*Claosaurus*" and *Diclonius*. It would appear, therefore, that as time progressed the skull in the *Hadrosaurinae*, as a general rule, became lower, culminating in the greatly depressed and very long skull of *Diclonius* in the closing days of the Cretaceous. The posterior height of the skull in *Edmontosaurus* is greater than the average among the genera of flat-headed hadrosaurs in which the head is known.

## LIST OF PRINCIPAL WORKS CITED.

- Hulke, J. W.—1871. Note on a large reptilian skull from Brooke, Isle of Wight, probably dinosaurian, and referable to the genus *Iguanodon*. Quart. Jour. Geol. Soc. London, vol. XXVII, pp. 199-206, pl. XI, figs. 1-5.
- Cope, E. D.—1883. On the characters of the skull in the *Hadrosauridae*. Proc. Acad. Nat. Sc. Philadel., vol. XXXV, pp. 97-107, pls. IV-VII.
- Andrews, Chas. W.—1897. Note on a cast of the brain-cavity of *Iguanodon*. Ann. and Mag. Nat. Hist., vol. XIX, sixth series, pp. 585-591, text fig. and pl. XVI, figs. 1-3.
- Hay, O. P.—1909. On the skull and the brain of *Triceratops*, with notes on the brain-cases of *Iguanodon* and *Megalosaurus*. Proc. U.S. Nat. Mus., vol. XXXVI, pp. 95-108, pls. 1-3.
- Gilmore, Charles W.—1909. Osteology of the Jurassic reptile *Campiosaurus*, with a revision of the species of the genus, and descriptions of two new species. Proc. U.S. Nat. Mus., vol. XXXVI, pp. 197-332, text figs. 1-48, pls. 6-20.
- Osborn, Henry Fairfield.—1912. Crania of *Tyrannosaurus* and *Allosaurus*. Mem. Am. Mus. Nat. Hist., new series, vol. I, pt. I, pp. 1-30, pls. I-IV, text figs. 1-27.
- Brown, B.—1914. *Anchiceratops*, a new genus of Horned dinosaurs from the Edmonton Cretaceous of Alberta. With discussion of the origin of the Ceratopsian crest and the brain-casts of *Anchiceratops* and *Trachodon*. Bull. Am. Mus. Nat. Hist., vol. XXXIII, pp. 539-548, text fig. 1, and pls. XXIX-XXXVII.
- Lambe, Lawrence M.—1917. A new genus and species of crestless hadrosaur from the Edmonton formation of Alberta. Ottawa Naturalist, vol. XXXI, pp. 65-73, pls. II and III.
- Lambe, Lawrence M.—1918. On the genus *Trachodon* of Leidy. Ottawa Naturalist, vol. XXXI, pp. 135-139.





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